Fire-Driven Extinction of Plant Populations: a Synthesis of Theory and Review of Evidence from Australian Vegetation

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Much of Australia's native vegetation is prone to recurring fires. Any desire to conserve the diversity of Australia's fire-prone plant communities must be backed by an understanding of how various regimes of fire affect processes that drive population and community change. Only with such understanding is it possible to predict which fire regimes are associated with high probabilities of population declines and extinctions so that these may be avoided in management. Several ecological concepts contribute to our ability to predict these outcomes. These include: description of temporal and spatial patterns of fires in terms of their frequency, intensity, season (fire regimes); characterisation and analysis of vegetation change in terms of population processes; and the definition of life-cycle attributes that allow species with similar responses to fire regimes to be classified into functional groups.

Using a demographic approach, I identified a number of fire-driven mechanisms of plant extinction. These include seven mechanisms related to death of standing plants and seeds, four mechanisms relating to failure of seed release and/or germination; four mechanisms relating to failure of seedling establishment; two mechanisms relating to the interruption of maturation or developmental growth; and three mechanisms relating to the failure of seed production. These processes may interact with each other, with co-occurring organisms, and with stochasticity in the physical environment. Such interactions may result in accelerated rates of population decline. Fire regimes associated with multiple mechanisms of plant population decline and extinction include high frequency fires, low frequency fires and repeated fires that result in little vertical penetration of heat and possibly smoke derivatives.

Many deficiencies remain in knowledge of the effects of fire on plant species and communities. Despite these deficiencies, mechanisms of plant extinction and the fire regimes with which they are associated are sufficiently well understood that they, along with existing theories of diversity and practical management tools, provide a strong scientific basis for the management of fire for conservation of plant populations and communities.

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INTRODUCTION

The influence of fire extends through virtually all terrestrial habitats in Australia, as it does in many other tropical and temperate parts of the world. In these areas fire may be viewed as an ecological process that mediates between maintenance and loss of biological diversity (Gill and Bradstock 1995). It is one of the few such processes that may be manipulated so readily (though not always successfully) by humans (Shea et al. 1981, van Wilgen et al. 1994, Bradstock et al. 1995), as indeed it has been over millennia to meet a wide variety of ends (Kohen, this volume). In Australia, conservation of biological diversity has become an explicit goal of contemporary fire management in many natural areas under public ownership (Shea et al. 1981, Conroy, this volume, Moore and Shields, this volume) and some areas under private ownership. The fulfilment of this goal, and its integration with other fire management goals, is contingent upon the use of knowledge on how fires affect ecological processes. With this knowledge, circumstances where fires cause loss of biological diversity can be *predicted*, so that they may be avoided or minimised in management practice (Bradstock et al. 1995). In this paper I review concepts that underpin predictive knowledge of the effects of fire, identify fire-driven mechanisms that cause plant populations to decline to extinction and examine some recent approaches to fire management directed at conservation. The emphasis here will be on plants (nomenclature of which follows Harden, 1990–1993) , while the effects of fire on animals is reviewed by Whelan et al. (this volume).

Concepts in fire ecology

1). Fire regimes

Gill (1975) introduced the concept of fire regimes, whereby sequences of recurring fires are characterised in terms of their frequency, intensity, season and fuel type. Fire regimes may thus be used to describe temporal patterns in the occurrence of fires over varying spatial scales across a landscape (e.g. Hobbs and Atkins 1988b, Gill and Bradstock 1995). Although some earlier workers had already begun to examine the ecological effects of fire explicitly in terms of the components of fire regimes (e.g. Gilbert 1959, Jackson 1968), many studies have taken a descriptive approach to fire ecology in which fires are viewed as single events followed by a process of recovery or succession (e.g. Jarret and Petrie 1929, Russell and Parsons 1978, Bell and Koch 1980). While the 'single fire' approach has yielded knowledge on ecological changes that occur during an interval between successive fires, it has contributed little to understanding changes that occur over a period interspersed by multiple fires (Morrison et al. 1995), which are the primary concern for conservation. The study of species responses in relation to fire regimes, rather than fire *per se*, is thus an essential basis for predictive knowledge on fire effects (Gill 1975, Noble and Slatyer 1981, Gill and Bradstock 1995).

2). The demographic processes underpinning ecosystem dynamics

Changes in the structure and composition of ecosystems are fundamentally driven by processes that operate within and between populations of organisms (Harper 1977). With an understanding of these fine-scale mechanisms, it should therefore be possible to predict outcomes in terms of composition, diversity and structure at higher levels of scale. Thus in this review I have taken a population approach (cf. Attiwill 1994), emphasising the effects of fire on survival, growth and reproduction within each stage of the plant life cycle (Fig. 1). A population may decline if fire causes the pool of individuals in each life stage to be reduced or interrupts the transfer of individuals between these stages. Extinction results when all pools decline to zero. In such an approach, the mechanisms and causes of population decline and extinction may be identified directly and consequent changes in community structure, composition and diversity may be logically predicted. It should be emphasised that interactions between species (e.g. competition, predation) and with the physical environment (e.g. through environmental stochasticity) are an essential component of a population approach (Fig. 1), as these factors may profoundly influence processes within populations (Harper 1977).

Studies of plant community structure, species composition and richness have a role in testing predicted outcomes of plant population processes (e.g. Morrison et al. 1995) but, on their own, are of limited value in generating predictive knowledge of fire-driven vegetation dynamics. Generalisations about dynamics that are derived from community patterns without reference to population processes as underlying mechanisms (e.g. Attiwill 1994) may sometimes lead to misinterpretations. The frequently cited observation of declining plant species richness with time since fire provides a cogent example. Decline in standing plant richness (e.g. Specht et al. 1958, Bell and Koch 1980) may reflect little or no loss of species from the community, depending on the richness of

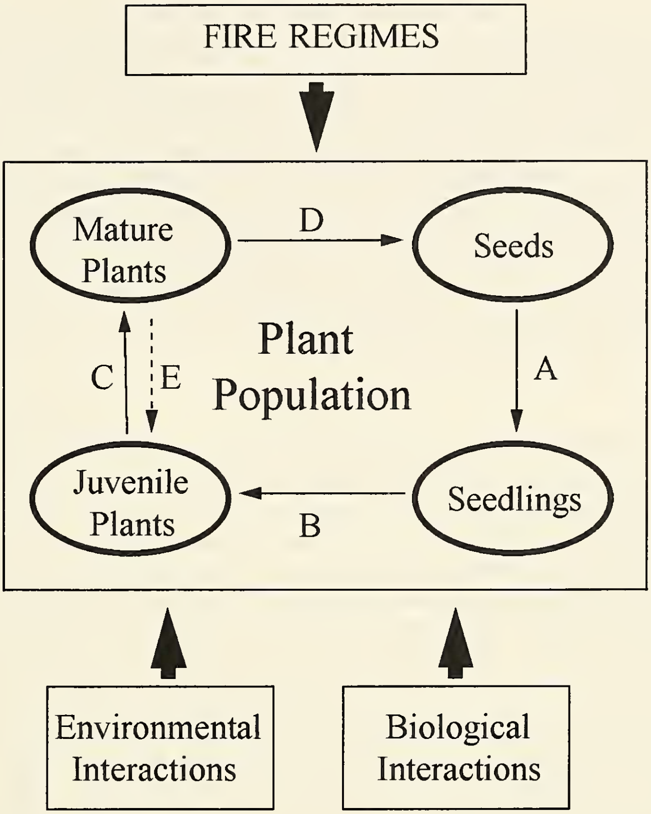

Fig 1. Diagrammatic representation of the processes involved in plant population dynamics of a flowering plant species (analogous schemes can be developed for non-flowering plants). Ellipses represent pools of individuals within each of four life stages. Arrows represent the flux of individuals between life stages: A — germination and emergence; B — seedling establishment; C — maturation and vegetative development; D — flowering, seed production and dispersal; E — establishment of vegetative propagules. Interactions with fire regimes, other organisms and the physical environment that influence rates of flux between life stages and rates of mortality within life stages are shown as arrows from external boxes. Interactions among these exogenous factors have been omitted for simplicity. Mechanisms of population decline and extinction are related to mortality in all life-stages (Mechanisms 1a–1g) and life-cycle fluxes as follows: A (Mechanisms 2a–2d); B and E (Mechanisms 3a–d); C (Mechanisms 4a–4b); and D (Mechanisms 5a–5c).

species represented in soil seed banks which may be substantial. The flux of individuals between these life stages (a population process) is often neglected, but is critical to the dynamics of vegetation after the next fire. It is also true that compositional studies may fail to detect effects of fire that may otherwise be evident from population studies (Lonsdale and Braithwaite 1991 *cf.* Bowman et al. 1988).

3). Life-history attributes

Life-history characteristics of plants vary greatly among species (e.g. Raunkaier 1934). The relevance of plant life history to fire response was discussed by Gill (1975, 1981), who identified traits such as the capacity to resprout after fire, fire stimulated release and germination of seed and post-fire flowering. Possession of particular life-history traits will determine the kinds of fire regimes likely to cause population decline by influencing the responses of particular life stages and rates of transfer between them

(Fig. 1). These traits will also determine which life stages or processes have a critical influence on the population response to particular fire regimes. Plant species that lack a capacity to resprout, for example, may be susceptible to decline under frequent fire regimes depending on the length of time required for maturation (see below).

Life-history attributes may be used to group species that have functionally similar fire responses and hence similar mechanisms of decline and extinction (Gill 1975, Noble and Slatyer 1980, Moore and Noble 1990, Keith 1991, Gill and Bradstock 1992, Keith and Bradstock 1994). Functional classifications of species offer a powerful means of ordering knowledge into generalisations (Verner 1984), as well as a guide for determining research priorities and applying fire management to species for which data are scarce. The latter is an important consideration, particularly in diverse ecosystems where species-by-species acquisition of knowledge may be desirable but is precluded by constraints on available research time and resources.

FIRE-DRIVEN MECHANISMS OF DECLINE/EXTINCTION IN PLANT POPULATIONS

Through each life stage represented in Fig. 1, there is a flux of individuals over time that may be broken down into several components (Harper 1977). Within a given time step, individuals in each life stage may have one of three fates: death; persistence within their present life stage; or passage into the next life stage. Individuals entering a given life stage from within the population must develop from the preceding stage. For mobile life stages (seeds and vegetative propagules), there may be additional fluxes of individuals to and from other populations. The relative magnitude of these fluxes determine whether a population will increase, decline or remain stable through time (Harper 1977).

The role of fire in the life cycles of plants is through its effect on survival of individuals in all life stages and its function as a cue for transfers between life stages. The cues provided by fire are critical for many plant species in which life-stage transfers (e.g. seed production, seed release, germination) do not operate continuously. Thus, a plant population may decline possibly to extinction whenever fire regimes interrupt the transfers between its life stages or deplete the pools of individuals within these life stages by mortality without commensurate replacement over an appropriate time scale (Fig. 1). The mechanisms through which these declines take place may be considered under five headings, depending on the life stages and processes that are affected (Fig. 1): death of standing plants and seeds; failure of seed release or germination; failure of seedling establishment; interruption of maturation and developmental growth; and failure of seed production. Below I examine how these mechanisms operate directly on individuals within plant populations and indirectly through interactions with the physical environment or populations of other organisms (Fig. 1) and identify a wide range of fire regimes implicated in decline and extinction of plant populations (Table 1). It should be noted that the processes discussed below do not act independently of one another. Rather, they interact within the context of whole populations, their habitat and associated species. I discuss the implications of these interactions in the next section (Vegetation Dynamics at Higher Levels of Organisation).

Death of Standing Plants and Seeds

There are at least seven mechanisms of plant population decline and extinction related to the death of standing plants and/or seeds caused by certain fire regimes (Table 1). Some of these mechanisms relate to fire regimes associated with the exposure of vital plant tissues to lethal temperatures (Mechanisms 1a, 1b and 1c, Table 1) or more gradual depletion of reserves essential for survival (Mechanism 1d). These regimes involve high intensity fires, fires causing penetration of high temperatures into the soil profile (i.e. due to consumption of extreme ground fuel loads and very long fire residence times), peat fires and high frequency fires. Other mechanisms relate to fire regimes involving long fire intervals that allow death through senescence or competitive elimination without commensurate replacement (Mechanisms 1e and 1f, Table 1).

Population declines and extinctions caused by fire-related mortality, where neither standing plants nor seeds survive in significant numbers are best known, both from direct observation and inference from historical evidence, in habitats that rarely experience fire. These include rainforests (e.g. Webb 1968, Ashton and Frankenberg 1976, Hill and Read 1984, Podger et al. 1988, Melick and Ashton 1991, Russell-Smith 1985, Russell-Smith and Bowman 1992) and alpine vegetation (e.g. Kirkpatrick 1983, Kirkpatrick and Dickinson 1984). However, high levels of fire-related mortality have been demonstrated in both standing plants (e.g. Noble 1989) and seed banks (e.g. Bradstock et al. 1994) of plant species typical of more fire-prone environments. Below I discuss evidence for each of these mechanisms and identify the environments and life-history types in which they are most likely to operate.

Survival under high fire temperatures depends on life-history characteristics. In some species fire may cause mortality of all standing plants in a population, given complete leaf scorch, so that population persistence is entirely dependent on seed (obligate seeders, Gill 1975). In other species a wide range of vegetative structures may confer the capacity for some or all standing plants to survive the passage of a fire by (i) protecting vital tissues from lethal temperatures; and (ii) harbouring buds that are the basis for vegetative recovery (resprouters, Gill 1975). The recovery buds in resprouters may be dormant (e.g. in mallee *Eucalyptus*) or actively growing (e.g. *Xanthorrhoea*) at the time of fire. Dormant seeds may similarly survive the passage of fire within storages known as seed banks.

In species that have neither a persistent seed bank nor vegetative structures allowing post-fire survival of standing plants, a single fire may cause catastrophic mortality. Some of the best known examples of these are alpine gymnosperms, particularly *Athrotaxis, Diselma, Microcachrys, Microstrobos* and *Podocarpus*, and the deciduous beech, *Nothofagus gunnii* (Kirkpatrick and Dickinson 1984). Other species lacking fire recovery traits are found in rainforests (e.g. Webb 1968, Melick and Ashton 1991), although a few examples (e.g. mistletoes) are known from more fire-prone environments (Gill 1981). Re-occupation of burnt sites by such species is dependent upon dispersal of propagules from unaffected populations (see below).

Mechanism 1a

Some woody shrubs and trees have recovery buds located above the ground. These include species with dormant epicormic buds protected by thick bark (e.g. most arborescent *Eucalyptus* species) and species with actively growing buds protected by crowded leaf bases (e.g. arborescent members of Arecaceae, Pandanaceae, Xanthorrhoeaceae and Kingiaceae). Seeds may also be stored above ground within woody fruits that are retained in the plant canopy for one or more years (see text on serotinous seed banks below). Temperatures to which aerial buds and seeds are exposed depend on fire intensity, the thickness of protective tissue and its thermal diffusivity (Gill and Ashton 1968, Vines 1968, McArthur 1968). Thus fires of high intensity will cause higher levels of mortality than those of low intensity (Mechanism 1a, Table 1), particularly among stems of trees or shrubs with thin or combustible bark (Penfold and Willis 1961, Cremer 1962, Gill 1981, Williams 1995) and among seeds within relatively thin-walled or unclustered fruits (Ashton 1986, Judd and Ashton 1991, Bradstock et al. 1994). The insulating properties of woody fruits may vary with age. Three year-old capsules of *Leptospermum continentale* (formerly included within *L. juniperinum*) subject to experimental heating reached lower internal maximum temperatures than one year-old fruits because their fruit walls were thicker and had greater moisture content, while *E. obliqua* showed the reverse response (Ashton 1986).

TABLE 1

Fire-driven mechanisms of plant population decline and extinction.

Life-cycle Process	Fire Regime Characteristics	Mechanism of Decline/Extinction	Life-history Types Affected
1. Death of standing plants & seeds	a) High intensity fires	Depletion of standing plants and seed banks through heat death of vital tissues above ground	Epicormic resprouters, passive fire tolerators and species with serotinous seed banks
	b) Fires consuming extreme quantities of ground fuel and with long residence times, especially when soil moisture is low	Depletion of standing plants and seed banks through heat death of vital tissues below ground	Resprouters, passive fire tolerators and species with soil seed banks. Especially when vital tissues are buried at shallow depths
	c) Peat fires	As for 1b.	As for 1b. Especially when peat is deep
	d) High frequency fires	Depletion of standing plants through depletion of bud banks, starch reserves or structural weakening	Resprouters and passive fire tolerators
	e) Low frequency fires	Depletion of standing plants and seed banks through senescence	Species with standing plants & seed banks that are short-lived relative to fire intervals
	f) Low frequency fires	Depletion of standing plants through competition with community dominants	Competitively subordinate species with short-lived seed banks
	g) High frequency fires	Depletion of standing plants through competition with opportunistic exotics	Species with slow-growing seedlings and resprouts in modified habitats
2. Failure of seed release and/or germination	a) Low frequency fires	Low rate of recruitment (relative to mortality) due to infrequent germination events	Species with limited seed release or germination in the absence of fire
	b) Low intensity fires	Low rate of recruitment (relative to mortality) due to release of few seeds	Species, especially trees, with serotinous seed banks and heat-dependent seed release
	c) Fires consuming small quantities of ground fuel and with short residence times, especially when soil moisture is high	Low rate of recruitment (relative to mortality) due to germination of few seeds caused by poor soil heating	Species with soil seed banks and heat-dependent dormancy
	d) Fires resulting in poor penetration of smoke derivatives into the soil profile	Low rate of recruitment (relative to mortality) due to germination of few seeds	Species with soil seed banks and smoke-dependent dormancy
3. Failure of seedling establishment	a) Low frequency fires	High mortality of seedlings emerging in the absence of fire due to resource deprivation, competition, predation and disease	Species whose seedlings are intolerant of conditions in 'mature' plant communities

	b) Fires preceding dry conditions (e.g. fires preceding summer, fires preceding drought)	High post-fire seedling mortality due to desiccation	Obligate seeders affected more rapidly than facultative seeders and vegetative increasers
	c) Extreme intensity fires, high frequency fires and peat fires with or without subsequent soil erosion	Physical change to habitat rendering it less amenable to seedling survival	Species occurring on organic or highly erodable substrates and in habitats rarely prone to fire
	d) Small or patchy fires and low intensity fires	High post-fire seedling mortality due to predation	Species with palatable seedlings. Obligate seeders affected more rapidly than facultative seeders and vegetative increasers
4. Interruption of maturation and developmental growth	a) High frequency fires	Fire-induced death of pre-reproductive juvenile plants	Obligate seeders affected more rapidly than resprouters
	b) High frequency fires	Fire-induced death of pre-resistant juvenile plants	Resprouters and passive fire tolerators
5. Failure of seed production	a) Low frequency fires	Low rate of recruitment due to infrequent flowering cues and seed production	Species whose flowering is stimulated only by the passage of fire
	b) Autumn/winter fires	Low rate of seed production (hence low recruitment rate) due to 'suboptimal' flowering cues	Species whose flowering is stimulated only by the passage of spring and summer fires
	c) Low frequency fires, small or patchy fires and low intensity fires	Low seed availability caused by high rates of predation (failure of predator satiation)	Species with fire-stimulated, flowering seed release or germination

Contrasting with species that survive fire actively by resprouting from dormant aerial buds protected from lethal temperatures are some arborescent obligate seeders whose actively growing shoots may avoid lethal temperatures (passive fire tolerators, Morrison 1995). Examples include *Leptospermum laevigatum* (Burrell 1981), species of *Callitris* (Bradstock 1989), *Allocasuarina littoralis, Acacia binervia* and *A. parramattensis* (Morrison 1995). These species may survive the passage of some fires if their actively growing canopy is held above scorch height and their bark is sufficiently thick within the scorch zone to protect vascular tissues from lethal temperatures. Operation of Mechanism 1a (Table 1) therefore depends on the developmental stage of the tree and flame height, which is related to fire intensity (Cheney 1981). Older trees with a high canopy, thick bark and discontinuous vertical fuel structure are more likely to survive than young trees (Morrison 1995).

Some plant species appear to influence community structure in a way that reduces the likelihood of lethal temperatures above ground during fires (Mechanism 1a, Table 1). In dense stands of some passive fire tolerators, such as *Allocasuarina littoralis* and *Callitris verrucosa*, heavy fall and compaction of litter and exclusion of understorey species may result in a ground fuel structure that reduces the chance of lethal canopy fires with post-fire age (Withers and Ashton 1977, Bradstock 1989). An analogous relationship may exist in alpine bolster heaths whose compact habit provides a fuel structure unfavourable to propagation of fire, allowing high rates of survival even when the margins of plants are scorched by ignition of adjacent fuels (Kirkpatrick 1983, Kirkpatrick and Dickinson 1984). Conversely, frequent firing may increase the ability of ground fuels to carry fire by stimulating vegetative recruitment in herbaceous resprouters, thereby increasing their density and possibly biomass. Tolhurst and Oswin (1992) demonstrated such a response in *Pteridium esculentum* when burnt by successive spring fires three years apart. Leigh and Noble (1981) also suggest a relationship between ground fuel structure and frequent fire in subalpine woodland, where high densities of leguminous shrubs may replace a less flammable groundcover of snow grass in response to frequent fire.

Mechanism 1b

In many resprouters the recovery organs, such as lignotubers (e.g. mallee *Eucalyptus*), bulbs, tubers, corms (e.g. various members of the Liliales) and rhizomes (e.g. various members of the Cyperaceae and Restionceae) are located underground. A large proportion of plant species (resprouters and obligate seeders) also have seed banks located underground (Auld 1994). Here, buds and seeds may be protected from lethal temperatures (Mechanism 1b, Table 1), not only by the insulating properties of the soil, but by the behaviour of fire which ensures that only about 5% of the heat that is generated travels in a downward direction (Packham 1970). The temperatures to which buried structures are elevated during the passage of fire are not directly related to fire intensity. Rather, these temperatures are related positively to the amount of ground fuel consumption and residence time of fire, and inversely to depth of burial and moisture content of soil at the time of fire (Beadle 1940, Bradstock et al. 1992, Valette et al. 1994, Bradstock and Auld 1995). These factors have, in turn, been related to levels of mortality among lignotubers of *Eucalyptus* (Noble 1984), *Banksia* (Bradstock and Myerscough 1988) and *Angophora* (Auld 1990), among rhizomes of several restionaceous sedges (Pate et al. 1991) and among soil-stored seed of native legumes (Auld 1987a, Auld and O'Connell 1991). Thus Mechanism 1b (Table 1) may be expected to operate on buried seeds and vegetative organs when depth of burial is shallow, ground fuel consumption is high, fire residence time is long and/or when soil moisture content is low.

Mechanism 1c

Where the soil itself is fuel, as is the case in peat fires, soil temperatures may reach 200 to 600°C and be sustained in that range for hours or days (Wein 1981, Frandsen 1991). Exposure to these levels and durations of heating causes high levels of mortality among standing plants (Mechanism 1c, Table 1) (Cremer 1962, Wein 1981, Hill 1982, Hill and Read 1984, Kirkpatrick and Dickinson 1984). Levels of mortality in soil seed banks are also likely to be high during peat fires (Wein 1981). The consequences of seed bank losses after peat fires have been examined in the northern hemisphere (e.g. Flinn and Wein 1977, Moore and Wein 1977), but few data exist for Australian plant communities (e.g. Cunningham and Cremer 1965). Hill and Read (1984), for example, inferred that seedlings of *Coprosma quadrifa* and *Pimelea drupacea* were confined to sites where peat remained unburnt because seeds stored in the soil were killed where the peat burned. The likelihood of peat combustion depends on its depth and moisture content (Wein 1981, Hill 1982).

A mechanism of fire evasion apparently operates in some species of trees subject to peat fires. Hill (1982) reported that tree mortality occurred where peat had combusted at their base, presumably killing their cambium (Cremer 1962), while trees generally survived where peat burnt incompletely around their base. Certain trees may evade death by: (i) having large irregularly shaped butts, increasing the chances of strips of cambium being sheltered from fire; or (ii) occurring preferentially in sites where peat depth is insufficient for combustion. Hill and Read (1984) suggested that these mechanisms, respectively, were responsible for rates of survival in *Eucalyptus nitida* and *Leptospermum scoparium* that were markedly higher than those of co-occurring rainforest tree species after a peat fire at Savage River, Tasmania. In a different fire, mortality among large trees of *Nothofagus cunninghamii* and *Eucryphia lucida* was higher than in smaller trees of the same species and *Atherosperma moschatum* and *Anodopetalum biglandulosum*. Hill (1982) suggested that these latter trees were more likely to evade lethal fires because of the shallower and less combustible accumulation of peat around their bases compared to large individuals of *N. cunninghamii* and *E. lucida*.

Mechanism 1d

Post-fire survival of standing plants may also depend on the distribution of recovery buds and/or the level of stored starch reserves (Pate et al. 1990, 1991). Resprouters may be killed if pools of dormant buds or stored starch reserves are exhausted by repeated fires or by fires at certain times of the annual growth cycle (Mechanism 1d, Table 1). Stands of mallee eucalypts, *E. incrassata*, a species that is well known for its resistance to fire, suffered extreme mortality when experimentally subjected to high-frequency fire (Noble 1989). The level of mortality increased with increasing fire frequency and reached a maximum of 95% after 4 successive fires one year apart (Noble 1989). *Stirlingia latifolia*, a resprouting heath shrub, is apparently more resilient to frequent fire regimes. Starch reserves held in its lignotuber were depleted by 50–75% in the period 2–5 months after a single fire, but were fully replenished by 1.5–2 years after fire (Bowen and Pate 1993). Starch reserves were exhausted, resulting in death, only after 10–12 monthly defoliation treatments. In *Banksia oblongifolia*, Zammit (1988) inferred that 70 % of dormant lignotuber buds were exhausted after a single clipping treatment and completely exhausted after four successive treatments, suggesting an intermediate level of resilience between *E. incrassata* and *S. latifolia*. However, pools of dormant buds were apparently restored after six months' growth. The ability to replenish dormant buds or starch reserves may diminish with age so that large old plants may suffer greater mortality in response to fire than younger, presumably more vigorous plants as observed, for example, in *Banksia grandis* (Burrows 1985). It has also been suggested that frequent fires cause tree death through structural weakening and eventual collapse (Benson 1985a) or by exposure of sensitive tissues to subsequent fires (Ashton and Frankenberg 1976, Russell-Smith and Dunlop 1987).

Noble's (1989) experiments also demonstrate the effect of fire season on mortality of standing plants. Repeated fires in spring resulted in lower mortality after 4 fires than repeated fires in autumn, presumably because spring fires preceded the annual growth season (summer–early autumn), whereas autumn fires coincided with a time when starch reserves had been depleted by recent growth (Noble 1989). Tolhurst and Oswin (1992) suggested that depletion of starch reserves may have been responsible for an observed reduction in density of *Poa sieberiana* after successive spring fires 3 years apart, relative to a single spring fire over the same period which resulted in increased density. A similar response to fire season may be expected in geophytic species, but I know of no available data on this topic.

Mechanism 1e

Fire may influence the number of individuals in various life stages of a plant population indirectly, through its absence, where transfers between these stages are dependent on fire (Fig. 1). If both standing plants and seeds are short-lived, and germination, seedling establishment or fruit production are constrained to the occurrence of fire (see below), then regimes of infrequent fire may cause decline and elimination of the population at a rate determined by senescence of standing plants and stored seeds (Mechanism 1e, Table 1). Many species with short-lived populations of standing plants apparently have persistent soil seed banks (e.g. Auld 1987a, though see Witkowski et al. 1991 for an exception, *Banksia coccinea*). Thus many reports that show a decrease in species richness of plant communities with time since fire (e.g. Specht et al. 1958, Russell and Parsons 1978, Bell and Koch 1980, Fox 1988) may be more likely to reflect a shift in the population structure of some species (i.e. from standing plants to buried seed), rather than a real loss of species from the community.

Survivorship or longevity data for standing plant populations in the absence of fire are available for a range of species (e.g. Ashton 1976, Lamont and Downes 1979, Wellington and Noble 1985a, Auld 1987a, Williams and Ashton 1988, Bradstock and

O'Connell 1988, Witkowski et al. 1991). The longevity of individual plants varies from less than a year in ephemeral herbs (e.g. Pate et al. 1985) to hundreds of years in woody perennials (e.g. Wellington et al. 1979, Lamont and Downes 1979, Head and Lacey 1988).

There are few data on the longevity of seed banks. Serotinous seed banks may persist for many years, but are unlikely to remain viable for long after senescence of parent plants (Gill and McMahon 1986, Witkowski et al. 1991, Lamont et al. 1991). Transient soil seed banks are even shorter-lived and have a discontinuous existence of a few months after flowering events (e.g. Gill and Ingwerson 1976, Auld 1987b, Auld 1990, Bradstock 1995). Experimental burial of seeds of forbs in the Asteraceae and Liliales that are typical of fire prone temperate grasslands yielded seed bank half-lives of two months to one year (Lunt 1995). Persistent soil seed banks may provide a basis for regeneration long after senescence of standing plant populations (e.g. Ewart 1908, Gilbert 1959). Auld (1994) summarised available data from burial experiments to estimate the longevity of persistent soil seed banks in fire-prone heath and woodland in the Sydney region. The results indicated a group of species with seed bank half-lives of 1–3 years duration (e.g. *Darwinia biflora, Zieria involucrata, Anisopogon avenaceus*), a group of species with seed bank half-lives in the order of a decade (e.g. *Acacia suaveolens, Grevillea linearifolia, Kunzea ambigua*) and a group of species with seed bank half-lives possibly in the order of several decades (e.g. *Gahnia sieberiana, Velleia perfoliata, Stackhousia viminea*). Inference from non-overlapping patterns of fruit production and seedling emergence at sites where dispersal from fruiting populations was unlikely also suggests that substantial quantities of buried seed of some herbaceous species may remain viable for well in excess of 10 years (e.g. Pate et al. 1985, Keith 1991, Lamont and Runciman 1993).

Mechanism 1f

Another mechanism of decline and extinction involves density-dependent interactions that lead to dominance of some species and competitive elimination of others as a consequence of resource deprivation (Keddy 1989). Competitive elimination (Mechanism 1f, Table 1) may be interrupted by disturbances, such as fire, if they allow recovery of suppressed individuals and recruitment of seedlings. Competitive effects may accelerate population declines that occur as a consequence of senescence, since both mechanisms operate during long fire intervals (1e and 1f, Table 1). However, these competitive interactions only affect the standing plant life stages of populations. Thus dormant propagules, depending on their longevity, may continue to persist in a community long after standing plants have been eliminated, perhaps to re-emerge as standing plants when fire reduces the biomass of the dominant species (Keith and Bradstock 1994).

Few Australian studies have examined the role of competition in terrestrial vegetation directly by experimental manipulation (e.g. Aarson and Epp 1990). Nonetheless, given sufficiently long fire-free intervals, there is evidence for decline and eventual competitive elimination of subdominant species in forests (e.g. Gilbert 1959, Ashton 1981), heathlands and woodlands (Withers 1979, Specht and Morgan 1981, Burrell 1981, Molnar et al. 1989, Keith and Bradstock 1994) and grasslands (Lunt 1991, Tremont and McIntyre 1994, Morgan 1994. in press). Species most prone to competitive elimination are subordinate in stature relative to community dominants and intolerant to conditions associated with the 'mature' community such as shade and leaf litter. Examples include interstitial herbs of grassland (Tremont and McIntyre 1994) and slow-growing sub-shrubs of heathlands (Keith and Bradstock 1994). Competitive elimination is also mediated by the structure of the community itself, particularly the density and spatial pattern of the dominant species which may be dependent on fire regimes and their spatial pattern, as well as seed dispersal mechanisms (Molnar et al. 1989, Lamont et al. 1993, Keith and Bradstock 1994, Morgan 1994).

Mechanism 1g

Where fires enhance invasion of herbaceous weeds they may cause decline and extinction of indigenous species through competition (Mechanism 1g, Table 1). By exploiting gaps and growing rapidly after fire, opportunistic weed species are able to exclude their slower growing neighbours from the community (McIntyre and Lavorel 1994). This mechanism of decline and extinction operates most rapidly under frequent fire regimes (Table 1), since these provide more gaps for the opportunists to exploit over a given time. Milberg and Lamont (1995), for example, showed experimentally how the abundance of exotic weeds increased at the expense of indigenous plant species after a single fire and that these changes persisted for at least 7 years. They suggested that increasing the frequency of fire would excerbate the transformation from native to exotic vegetation. Similar conclusions were reached by Hobbs and Atkins (1990). Some plant communities are apparently less susceptible to weed invasion after fire than others, since dispersal of weed propagules into burnt areas is not always followed by establishment (Hobbs and Atkins 1988a, Hester and Hobbs 1992). The reasons for these differences apparently involve other sources of disturbance that cause habitat modification as commonly occurs in agricultural and urban landscapes. These include water and nutrient enrichment, increased herbivory and physical disturbance to vegetation (Tremont and McIntyre 1994, McIntyre and Lavorel 1994).

Failure of Seed Release and/or Germination

These mechanisms of decline and extinction relate to the part of the plant life cycle where individuals are transferred from stored seeds to seedlings (Fig. 1). Certain kinds of fires provide cues to release seeds from serotinous seed banks and to break dormancy of seeds in soil seed banks, resulting in mass germination events (Gill 1981). Fire regimes that fail to provide cues that stimulate the release and germination of seeds at a rate sufficient to replace deaths of standing plants will cause a plant population to decline, possibly to extinction. This may occur if fire regimes stimulate germination infrequently or if they result in germination events that involve relatively few seeds. In the first instance declines and extinctions may be associated with infrequent fire regimes (Mechanism 2a, Table 1). In the second instance declines and extinctions may be associated with aspects of fire behaviour that influence the generation of heat and the dispersal of smoke and ash (Mechanisms 2b–d, Table 1), since these in turn influence the size and timing of germination events (Auld and O'Connell 1991, Dixon et al. 1995). The critical aspects of fire behaviour depend on whether seed storage is in the plant canopy or in the soil and on the nature of seed dormancy.

Mechanism 2a

When fires occur infrequently, there will be few opportunities for seed release or germination, thereby limiting seedling recruitment, so that a population may decline at a rate determined by the rate of death in each life stage (Mechanism 2a, Table 1). Where death rates among standing plants and seeds are high (i.e. where all life-stages are short-lived), frequent germination events that involve large numbers of seeds are required if population decline is to be avoided, unless deaths are offset by immigration. Conversely, where death rates are low, infrequent germination events or those that involve small numbers of seeds may be sufficient to maintain population stability.

Operation of Mechanism 2a (and Mechanisms 2b–d) may be offset if the rate of spontaneous seed release and germination (i.e. the extent to which seeds germinate independently of fires) is substantial and results in seedling recruitment. The extent to which the availability of seeds for germination is constrained by the occurrence of fire varies among both serotinous species and those with soil seed banks. Seeds may be released and germinate independently of fire either through spontaneous release of seeds from woody fruits (Ashton 1979, Abbott 1985, Cowling and Lamont 1985a, Wellington and Noble 1985a, Bradstock and O'Connell 1988, Lamont and van Leeuwin 1988, Zammit and Westoby 1988, Enright and Lamont 1989b, Bradstock 1990, Davies and Myerscough 1991, Pannell 1995), by continued production of a fraction of non-dormant seeds (Auld and O'Connell 1991, Morrison et al. 1992) or by spontaneous release from dormancy

(Baskin and Baskin 1989, Morrison et al. 1992, Auld et al. 1993). An obvious corollary of spontaneous germination is depletion of regeneration capacity after the next fire, particularly if germinated seeds fail to grow into established plants, because these seeds are lost from storage and will not contribute to any subsequent post-fire germination event.

The extent to which seeds are retained in serotinous fruits until fire or released spontaneously through time varies between and within species. Spontaneous release of seed from serotinous seed banks may occur when fruits are desiccated during branch senescence or in response to wet–dry cycles. Davies and Myerscough (1991), for example, estimated that serotinous seed in *Eucalyptus luehmanniana* had a turnover time of 1–2 years. Wet–dry cycles were apparently responsible for spontaneous release of 90% of seeds independently of fire in the first year after fruit maturation in *Banksia grandis* (Abbott 1985). Cowling and Lamont (1985a) demonstrated that levels of serotiny varied within *Banksia* species in relation to moisture status of the habitat, xeric habitats supporting populations with more serotinous seed banks.

Levels of dormancy in soil seed banks vary between populations and with seed age (Bradstock 1989 *cf.* Bogusiak et al. 1990, Auld and O'Connell 1991, Morrison et al. 1992, Auld et al. 1993, Bell et al. 1993, Dixon et al. 1995). This variation is attributable to several different mechanisms and may contribute to a substantial capacity for germination independent of fire. Auld and O'Connell (1991) reported that the non-dormant fraction of annual seed lots varied between zero and 59% among 35 native legume species. In some species the non-dormant fraction of seeds is small at the time of release but increases with seed age, a process that has been attributed to mechanical abrasion, action of digestive juices, microbial or fungal attack, high or fluctuating ambient temperatures and high relative humidity (e.g. Mott 1972, Cavanagh 1987). Morrison et al. (1992) found that seed dormancy may also decrease in dry storage, a process known as after-ripening. They detected after-ripening over three years in several species of legumes in the tribes Bossiaeeae and Phaseoleae, but not in numerous species from other tribes of the family. Finally, there is a possibility that seed dormancy may vary in a reversible manner. Auld et al. (1993) found that dormancy of experimentally buried seeds of *Darwinia* and *Grevillea* was reduced over summer, but restored in the following winter.

Mechanism 2b

Species of Proteaceae (*Banksia, Dryandra, Hakea, Petrophile, Isopogon, Strangea, Xylomelum*), Myrtaceae (*Eucalyptus, Leptospermum, Melaleuca, Callistemon, Kunzea, Agonis, Astartea, Calothamnus, Beaufortia, Eremea, Regelia, Phymatocarpus, Pericalymma*), Casuarinaceae (*Casuarina, Allocasuarina*) and Cupressaceae (*Callitris, Actinostrobos*) have serotinous seed banks. In many of these taxa, seed release occurs whenever the fruit is desiccated, as is the case when their branches are scorched by fire. Thus, low intensity fires may result in only partial seed release if scorching does not reach the height of some or all fruit-bearing branches, unless the entire plant is killed by basal scorching. The outcome may be limited seedling recruitment and population decline (Mechanism 2b, Table 1).

In many *Banksia* species, release of seeds requires exposure to temperatures well above ambient levels to rupture an abscission zone of cells in the fruit (Gill 1976). The temperature to which *Banksia* fruits are exposed affects not only the ultimate proportion of seeds released, but also their rate of release over the first post-fire year (Bradstock and Bedward 1992), a factor that may have implications for seedling survival (see next section). Enright and Lamont (1989a) have shown that threshold temperatures required for 90% seed release varied from 175 to 500°C among 10 *Banksia* species. Temperature-dependent seed release was also shown by Zammit and Westoby (1987a). Low intensity fires are less likely to produce temperatures required for seed release than high intensity fires, particularly where serotinous fruits are held high above the ground. Mechanism 2b (Table 1) is therefore likely to be associated with more rapid population declines in serotinous species with arborescent growth forms than in those with non-arborescent growth forms.

Mechanism 2c

The widely observed phenomenon of pulsed post-fire seedling recruitment (Specht et al. 1958, Purdie 1977b, Hobbs and Atkins 1990, Clark 1988, Tolhurst and Oswin 1992, Auld and Tozer 1995) suggests that large numbers of species in fire-prone environments have soil seed banks whose dormancy is broken by fire-related cues. Seed dormancy mechanisms are well known in leguminous species: seeds have hard impermeable seed coats which may be ruptured by heat or physical damage, allowing them to imbibe and germinate (Baskin and Baskin 1989). A germination response to heat has been demonstrated in a wide range of Australian legumes and other taxa (Table 2). Auld and O'Connell (1991) have shown that threshold temperatures for germination varied from 40 to 80°C among 34 legume species, while germination response was relatively insensitive to duration of exposure to these temperatures. Fires consuming 0.6 to 2.0 $kg.m^{-2}$ of fine ground fuel are required to generate these temperatures to depths of 1–3 cm below ground surface (Bradstock et al. 1992, Bradstock and Auld 1995), where most soil seed capable of emergence is located (Auld 1986a, unpubl. data). Fires that fail to meet these conditions may be associated with low levels of germination from soil seed banks and hence population declines (Mechanism 2c,Table 1).

TABLE 2

Genera with persistent soil seed banks for which an enhanced germination response to heat (H) or smoke (S) have been demonstrated experimentally and genera in which such responses have been tested but not found (h and s, respectively). Results should be treated with some caution because experimental methods vary between authors and responses are likely to vary within genera, species and populations.

Genus	Family	Response	Source
Acacia	Fabaceae	H	Beadle 1940, Floyd 1966, 1976, Shea et al. 1979, Warcup 1980, Vlahos and Bell 1986, Auld 1987a, Hodgkinson and Oxley 1990, Auld and O'Connell 1991, Bell et al. 1993
Actinodium	Myrtaceae	s	Dixon et al. 1995
Actinostrobos	Cupressaceae	S	Dixon et al. 1995
Actinotus	Apiaceae	H	Auld, Bradstock and Keith, unpubl.
Adriana	Euphorbiaceae	s	Dixon et al. 1995
Agrostocrinum	Anthericaceae	s	Dixon et al. 1995
Alogyne	Malvaceae	s	Dixon et al. 1995
Amphipogon	Poaceae	s	Dixon et al. 1995
Andersonia	Epacridaceae	S	Dixon et al. 1995
Anigozanthos	Haemodoraceae	S	Dixon et al. 1995
Anisopogon	Poaceae	h	Auld, Bradstock and Keith, unpubl.
Anthibolus	Santalaceae	s	Dixon et al. 1995
Aotus	Fabaceae	H	Auld and O'Connell 1991
Asterolasia	Rutaceae	H	Auld, unpubl.
Astroloma	Epacridaceae	s	Dixon et al. 1995
Billardiera	Pittosporaceae	S	Dixon et al. 1995
Blandfordia		h	Auld, Bradstock and Keith, unpubl.
Boronia	Rutaceae	s	Dixon et al. 1995
		H	Auld, Bradstock and Keith, unpubl.
Bossiaea	Fabaceae	H	Warcup 1980, Auld and O'Connell 1991, Bell et al. 1993
Brachyloma	Epacridaceae	s	Dixon et al. 1995
Burchardia	Colchicaceae	S	Dixon et al. 1995
		h	Auld, Bradstock and Keith, unpubl.
Chamaescilla	Anthericaceae	S	Dixon et al. 1995
Choretrum	Santalaceae	s	Dixon et al. 1995

Chorizema	Fabaceae	H	Bell et al. 1993
Codonocarpus	Gyrostemonaceae	S	Dixon et al. 1995
Comesperma	Polygalaceae	H	Auld, Bradstock and Keith, unpubl.
Commersonia	Sterculiaceae	H	Floyd 1976
Conospermum	Proteaceae	S	Dixon et al. 1995
		H	Auld, Bradstock and Keith, unpubl.
Conostephium	Epacridaceae	s	Dixon et al. 1995
Conostylis	Haemodoraceae	H	Bell et al. 1987, Bell et al. 1993,
		S	Dixon et al. 1995
Convolvulus	Convolvulaceae	H	Warcup 1980
Croninia	Epacridaceae	s	Dixon et al. 1995
Darwinia	Myrtaceae	H,h	Auld et al. 1991, 1993
Daviesia	Fabaceae	H	Auld and O'Connell 1991, Bell et al. 1993
Deyeuxia	Poaceae	H	Warcup 1980
Dichondra	Convolvulaceae	H	Warcup 1980
Dillwynia	Fabaceae	H	Auld and O'Connell 1991
Dodonaea	Sapindaceae	H	Floyd 1966, 1976, Warcup 1980, Hodgkinson and Oxley 1990, Auld, Bradstock and Keith, unpubl.
Drosera	Droseraceae	s	Dixon et al. 1995
Epacris	Epacridaceae	H	Warcup 1980, Auld, Bradstock and Keith unpubl.
Eriostemon	Rutaceae	S	Dixon et al. 1995
Exocarpos	Santalaceae	s	Dixon et al. 1995
Gahnia	Cyperceae	h	Auld, Bradstock and Keith unpubl.
		s	Dixon et al. 1995
Gastrolobium	Fabaceae	H	Bell et al. 1993
Geleznowia	Rutaceae	S	Dixon et al. 1995
Geranium	Geraniaceae	H	Warcup 1980
Glycine	Fabaceae	H	Auld and O'Connell 1991
Gompholobium	Fabaceae	H	Vlahos and Bell 1986, Auld and O'Connell 1991, Bell et al. 1993
Goodenia	Goodeniaceae	s	Dixon et al. 1995
Grevillea	Proteaeceae	S	Dixon et al. 1995
		h	Auld and Tozer 1995
Gyrostemon	Gyrostemonaceae	S	Dixon et al. 1995
Hardenbergia	Fabaceae	H	Auld and O'Connell 1991, Bell et al. 1993
Hemiandra	Lamiaceae	s	Dixon et al. 1995
Hibbertia	Dilleniaceae	S	Dixon et al. 1995
		h	Auld, Bradstock and Keith, unpubl.
Hovea	Fabaceae	H	Vlahos and Bell 1986, Bell et al. 1993
Hybanthus	Violaceae	S	Dixon et al. 1995
Hypocalyma	Myrtaceae	S	Dixon et al. 1995
Isolepis	Cyperaceae	H	Warcup 1980
Jacksonia	Fabaceae	H	Bell et al. 1993
Johnsonia	Anthericaceae	s	Dixon et al. 1995
Juncus	Juncaceae	H	Warcup 1980
Kennedia	Fabaceae	H	Floyd 1966, 1976, Vlahos and Bell 1986, Auld and O'Connell 1991, Bell et al. 1993
Kunzea	Myrtaceae	H	Auld, Bradstock and Keith unpubl.
Lachnostachys	Chloanthaceae	s	Dixon et al. 1995
Lepidosperma	Cyperaceae	s	Dixon et al. 1995
Leschnaultia	Goodeniacaeae	S	Dixon et al. 1995
Leucopogon	Epacridaceae	s	Dixon et al. 1995
Lomandra	Lomandraceae	s	Dixon et al. 1995
Lysinema	Epacridaceae	S	Dixon et al. 1995
Macropidia	Haemodoraceae	s	Dixon et al. 1995

Mirbelia	Fabaceae	H	Shea et al. 1979, Auld and O'Connell 1991, Bell et al. 1993
Neurachne	Poaceae	S	Dixon et al. 1995
Olearia	Asteraceae	h	Auld, unpubl.
Opercularia	Rubiaceae	H	Warcup 1980
Oxylobium	Fabaceae	H	Bell et al. 1993
Ozothamnus	Asteraceae	H	Floyd 1976
Paraserianthes	Fabaceae	H	Bell et al. 1993
Patersonia	Iridaceae	S	Dixon et al. 1995
Pelargonium	Geraniaceae	H	Warcup 1980
Persoonia	Proteaeceae	s	Dixon et al. 1995
		h	Auld, Bradstock and Keith, unpubl.
Petrophile	Proteaceae	S	Dixon et al. 1995
Phebalium	Rutaceae	s	Dixon et al. 1995
Phyllota	Fabaceae	H	Auld and O'Connell 1991
Pimelea	Thymelaeaceae	H	Auld, Bradstock and Keith unpubl.
		S	Dixon et al. 1995
Platylobium	Fabaceae	H	Auld and O'Connell 1991
Platysace	Apiaceae	H	Warcup 1980
Pomaderris	Rhamnaceae	H	Warcup 1980, Coates 1991, Auld, Bradstock and Keith, unpubl.
Poranthera	Euphorbiacae	H	Warcup 1980
Pultenaea	Fabaceae	H	Warcup 1980, Auld and O'Connell 1991
Ricinocarpos	Euphorbiaceae	h	Auld, Bradstock and Keith, unpubl.
Rulingia	Sterculiaceae	S	Dixon et al. 1995
Scaevola	Goodeniaceae	S	Dixon et al. 1995
Scholtzia	Myrtaceae	s	Dixon et al. 1995
Senna	Fabaceae	H	Hodgkinson and Oxley 1990
Seringia	Sterculiaceae	H	Floyd 1976
Siegfriedia	Rhamnaceae	S	Dixon et al. 1995
Sorghum	Poaceae	H	Andrew and Mott 1983
Sowerbaea	Anthericaceae	s	Dixon et al. 1995
Sphaerolobium	Fabaceae	H	Auld and O'Connell 1991, Bell et al. 1993
Sphenotoma	Epacridaceae	S	Dixon et al. 1995
Sprengelia	Epacridaceae	H	Warcup 1980, Auld, Bradstock and Keith unpubl.
Spyridium	Rhamnaceae	H	Warcup 1980
		S	Dixon et al. 1995
Stackhousia	Stackhousiaceae	S	Dixon et al. 1995
		H	Auld, Bradstock and Keith, unpubl.
Stirlingia	Proteaeceae	S	Dixon et al. 1995
Stylidium	Stylidiaceae	H	Tozer, unpubl.
Styphelia	Epacridaceae	s	Dixon et al. 1995
Synaphea	Proteaceae	s	Dixon et al. 1995
Tetratheca	Tremandraceae	S	Dixon et al. 1995
Thomasia	Sterculiaceae	s	Dixon et al. 1995
Thysanotus	Anthericaceae	S	Dixon et al. 1995
Tripterococcus	Stackhousiaceae	s	Dixon et al. 1995
Trymalium	Rhamnaceae	H	Bell et al. 1987
Velleia	Goodeniaceae	H	Auld unpubl.
		s	Dixon et al. 1995
Verticordia	Myrtaceae	S	Dixon et al. 1995
Viminaria	Fabaceae	H	Auld and O'Connell 1991, Bell et al. 1993
Xanthorrhoea	Xanthorrhoeaceae	h	Auld, Bradstock and Keith, unpubl.
Xanthosia	Apiaceae	s	Dixon et al. 1995
Zieria	Rutaceae	H	Floyd 1976, Auld unpubl.

Mechanism 2d

Fire-related germination cues other than heat include chemical responses from smoke (van der Venter and Esterhuizen 1988, de Lange and Boucher 1990, Brown 1993, Dixon et al. 1995) and charred wood (Keeley et al. 1985, Keeley and Pizzorno 1986). The active chemical agents within smoke are not known, but are apparently widespread in occurrence and act relatively indiscriminately on germination across a wide range of taxa (Dixon et al. 1995). Dixon et al. (1995) found positive germination responses to smoke in 45 of 94 south-western Australian plant taxa, some of which also responded positively to heat (Table 2). They suggested that seed banks of certain species may require exposure sequentially or possibly additively to a number of stimuli before dormancy is broken. However, approximately half of the taxa exhibiting a positive germination response to smoke were not germinable by other means and several others showed greater germinability after smoke treatment than after heat treatment (Dixon et al. 1995). Further, Dixon et al. (1995) were able to stimulate additional seedling emergence from residual seed banks in recently burnt areas by applying smoke experimentally to the soil *in situ* using fumigation apparatus. The experimental site had been previously burnt by a low intensity fire which presumably resulted in little penetration of heat or smoke derivatives into the soil profile.

The factors affecting generation of smoke derivatives and their penetration into the soil profile are currently unknown, but are likely to be critical in the determining the magnitude of germination responses and hence the likelihood of population declines (Mechanism 2d, Table 1). Given that heat and smoke derivatives may penetrate the soil profile in different ways, smoke derivatives may be important in breaking dormancy of seeds buried at depths beyond those subject to elevated temperatures during fire (e.g. Bradstock and Auld 1995).

Failure of Seedling Establishment

Seedling establishment refers to the transfer of individuals from the seedling stage to the juvenile stage (Fig. 1). If seedling establishment fails to replace deaths among standing plants over time, a population will decline, possibly to extinction. There are at least four mechanisms by which fire regimes may cause population declines and extinctions by limiting seedling establishment (Fig. 1, Table 1). Infrequent fire regimes may limit seedling recruitment by limiting the number of opportunities for establishment, assuming the timing of seedling establishment is constrained to the immediate post-fire period (Mechanism 3a, Table 1). In many species seedling establishment is at least partly constrained to the immediate post-fire period by mechanisms of seed release and dormancy (see preceding section). Below I examine processes affecting seedling survival that act to further constrain seedling survival to the post-fire period. Other mechanisms of population decline and extinction involve limitations on seedling survival in the post-fire environment imposed by limited moisture supply (Mechanism 3b, Table 1), physical changes to the habitat wrought by extreme fire events (Mechanism 3c, Table 1) and predators (Mechanism 3d, Table 1).

Mechanism 3a

Evidence that seedling establishment is greater immediately after fire than in an established (unburnt) community has been documented in Australian forests (Beadle 1940, Christensen and Kimber 1975, Ashton 1976, Hill and Read 1984, Tolhurst and Oswin 1992), woodlands (Purdie 1977b, Withers 1978, 1979, Clark 1988, Hobbs and Atkins 1990, Auld and Tozer 1995), heathlands (Beadle 1940, Specht et al. 1958, Zammit and Westoby 1987a, Cowling and Lamont 1987, Meney et al. 1994), swamps (Keith 1991), grasslands (Westoby et al. 1988, Gilfedder and Kirkpatrick 1993, Tremont and McIntyre 1994, Morgan in press) and arid and semi-arid shrublands (Griffin and Friedel 1984, Wellington and Noble 1985a, Hodgkinson 1991). In combination, intolerance to shade and increased susceptibility to fungal pathogens, desiccation and predators may severely limit seedling establishment of many species in a wide range of habitats, except when the passage of a fire liberates resources (particularly light, water and nutrients), reduces competition and facilitates predator satiation. Where fires occur rarely, as in low frequency fire regimes, population declines may occur at a rate determined by the mortality of standing plants (Mechanism 3a, Table 1).

Prolonged exposure to shade and consequent fungal disease have been implicated as major factors responsible for high seedling mortality in the absence of fire in wet forest eucalypts (Gilbert 1959, Ashton and MacCauley 1972), in a range of understorey species and eucalypts of dry grassy woodlands (Purdie 1977b, Withers 1978, 1979) and in fire-prone swamp vegetation (Keith 1991). In the latter community high seedling mortality is correlated with a dense canopy of resprouting graminoids and ferns that reduces light intensity at the soil surface by two orders of magnitude (Keith 1991). Desiccation is a second cause of high mortality of seedlings in unburnt vegetation. Studies of heathlands on both sides of the continent showed mortality of newly emerged *Banksia* seedlings was significantly higher in vegetation unburnt for at least 3 years compared with vegetation burnt immediately prior to sowing and this difference was ascribed to desiccation (Cowling and Lamont 1987, Zammit and Westoby 1988). Similar differences in seedling mortality have also been ascribed to desiccation in a diverse range of species and habitats: epacridaceous shrubs and restionaceous sedges in heathland (Meney et al. 1994); numerous eucalypt and understorey species in temperate woodlands (Purdie 1977b, Withers 1978, Auld 1987a, Davies and Myerscough 1991, Tozer unpubl.); and mallee eucalypts and shrubs in semi-arid shrublands (Wellington and Noble 1985a,b, Bradstock 1989). In all cases few or none of the seedlings in unburnt vegetation survived the first summer after emergence, while a larger but variable fraction survived to become established in recently burnt vegetation. Predation is another cause of seedling mortality that appears to have a greater impact in unburnt conditions than after a recent fire (Purdie 1977b, Wellington and Noble 1985a,b, Bradstock 1989). Similar fire-mediated predator satiation may operate on newly emerged seedlings to that described below for post-dispersal seeds (see text on Mechanism 5c).

Some species are apparently capable of spontaneous seedling establishment in 'mature' unburnt communities at rates that may be sufficient to prevent population declines through Mechanism 3a (Table 1). Ashton (1976) recorded substantial recruitment of woody understorey species, notably *Coprosma quadrifida* and *Cyathea australis*, between 28 and 48 years post-fire in a regenerating south-eastern Australian forest. This appears to be a common phenomenon among rainforest elements in the understoreys of wet eucalypt forests (Webb 1968, Ashton 1976, Ashton and Frankenberg 1976, Read and Hill 1988). Similarly, Abbott (1985) observed continuous recruitment of seedlings of *Banksia grandis* in wet eucalypt forests of south-western Australia, apparently at a rate sufficient for populations to persist in the absence of fire. Species of *Allocasuarina* and *Acacia* are apparently capable of persistence by continual recruitment in the absence of fire, even though growth rates are 1.5 to 5 times slower than in burnt sites (Withers and Ashton 1977, Withers 1978). In tropical savanna woodlands seedling recruitment occurs seasonally and independent of fire in annual grasses (e.g. Andrew and Mott 1983, Mott and Andrew 1985) and some trees and shrubs (Price and Bowman 1994). Spontaneous recruitment appears to be very uncommon in heathlands. *Leptospermum laevigatum* is able to recruit seedlings and invade heathland in the absence of fire, however, its establishment may be aided by other forms of disturbance such as grazing and past clearing activities (Burrell 1981, Bennett 1994). Indeed, Australian heathlands, appear to be unique among temperate heathlands globally, in having very few woody species able to recruit seedlings in the absence of fire (Keeley 1995).

The senescence of dominant plants in a community may create conditions suitable for seedling establishment where this is otherwise limited in 'mature communities' by scarcity of light and space. Data on the dynamics of long unburnt plant populations in Australian fire-prone habitats are scarce but there is evidence for seedling recruitment into small gaps caused by senescence in rainforests (Webb 1968), eucalypt forests (Abbott 1985) and woodlands (Withers 1978, 1979), lowland heaths (Witkowski et al. 1991), subalpine heaths (Williams and Ashton 1988) and grasslands (Tremont and McIntyre 1994, Morgan in press). Nonetheless, for the majority of species in these habitats except rainforests, recruitment that may occur in long unburnt stands is unlikely to be sufficient to replace spontaneous deaths of standing plants (e.g. Withers 1978,1989, Ashton 1981, Gill and McMahon 1986, Bradstock and O'Connell 1988, Williams and Ashton 1988, Bradstock 1990, Witkowski et al. 1991, Burgman and Lamont 1992).

The relationship between the occurrence of fire and vegetative recruitment in clonal species (Fig. 1) may be analogous to that between fire and seedling recruitment. Few data exist on this topic, but there is evidence of increased vegetative recruitment after fire in *Pteridium esculentum* (Tolhurst and Oswin 1992, Tolhurst and Burgman 1994) and members of the Haemodoraceae (Lamont and Runciman 1993). In *P. esculentum*, vegetative recruitment appears to increase with fire frequency, since the annual rate of recruitment decreases with time since fire. Vegetative recruitment is influenced by fire season, increases in recruitment being greater and sustained for longer after spring fires than after autumn fires (Tolhurst and Oswin 1992). However, it is not known whether exclusion of fire over a long period results in continued decline in density and eventual elimination of any species dependent on vegetative recruitment. Thus, further research is necessary to determine the applicability of Mechanism 3a (Table 1) to clonal species.

Mechanism 3b

The role of soil moisture in seedling mortality (e.g. Wellington and Noble 1985a, Cowling and Lamont 1987, Bradstock and O'Connell 1988), suggests that opportunities for seedling recruitment may be constrained not only by the occurrence of fire, but the weather conditions that follow it. Population declines and extinctions are likely where fires are followed by dry conditions in the first year, curtailing the rate of recruitment (Mechanism 3b, Table 1). The likelihood of conditions unfavourable to seedling establishment is influenced by season of fire (on average, declines are more likely in response to winter and spring fires than fires in other seasons), as well as year to year variations in weather and fine-scale spatial variability in availability of moisture and nutrients.

Several authors have emphasised the stochastic nature of the relationship between the occurrence of fire, post-fire rainfall and seedling recruitment (Bradstock and Bedward 1992, Burgman and Lamont 1992). The coincidence of events when a fire is followed by a sequence of seasons suitable for germination and seedling establishment is likely to be rare in some habitats. Wellington and Noble (1985a), for example, estimated that recruitment of *Eucalyptus incrassata* occurred after only about 10% of fires. In south-western Australia where there is a predictable mean winter maximum rainfall, seedling recruitment varies substantially in response to fire season. Seedlings emerging after fires in spring are exposed to hot dry conditions at a younger age than those emerging after fires in summer or autumn and consequently suffer greater rates of mortality (Cowling and Lamont 1987, Cowling et al. 1990, Hobbs and Atkins 1990, Lamont et al. 1991). A similar trend has been demonstrated in South Africa (Bond et al. 1984). However in eastern Australia, where rainfall is less predictably seasonal and has a mean summer maximum, the response of recruitment to fire season, although still evident, is weaker (Clark 1988, Hodgkinson 1991, Tolhurst and Oswin 1992, Bradstock and Bedward 1992, Whelan and Tait 1995). As a consequence, fires in summer and autumn may sometimes be less favourable to seedling recruitment than fires in winter and spring (e.g. Noble 1989, Whelan and Tait 1995), even though the reverse is more usually true. Factors that influence the timing of seed release and germination may also offset seasonal effects on desiccation of seedlings. Cowling and Lamont (1985b) suggested that wet–dry cycles had a role in regulating the season of seed release after fire. Wet–dry cycles resulted in greater seed release under cool ambient temperatures (15–20°C) than warm temperatures (c. 20°C), so that more rapid seed release would be expected in autumn than in spring or summer (Cowling and Lamont 1985b, Enright and Lamont 1989a). Secondary dormancy mechanisms related to ambient temperature may have a similar role (e.g. Andrew and Mott 1983, Mott and Andrew 1985, Bradstock and Bedward 1992).

An analogous relationship may exist between spatial variability in resource supply and the establishment and maturation of seedlings. Sites with locally abundant supplies of moisture or nutrients may favour higher rates of seedling establishment (Tongway et al. 1989, Tongway and Ludwig 1990) and maturation (Keith unpubl. data) and thus act as important refuges or core habitat for plant populations under adverse fire regimes. In some cases, however, the advantages to growth and maturation in resource-rich patches may be offset by other interactions such as competition (Morris and Myerscough 1988, Lamont et al. 1993).

Mechanism 3c

Certain fire regimes or even single fire events may modify some landscapes in a way that makes them no longer suitable for habitation by certain plant species, particularly through the prevention of seedling establishment (Mechanism 3c, Table 1). Fires associated with habitat change may also cause extreme mortality in all life stages of the population (Mechanism 1a, Table 1), resulting in sudden and long-lasting local extinctions. The fire regime itself may change physical characteristics of the habitat either directly, or in concert with other events such as erosive rainfall (Table 1). The best examples of this mechanism of extinction come from habitats where fire may be a rare phenomenon such as peatlands, alpine vegetation, rainforests and, to a lesser extent deserts.

Peat fires may expose coarse gravel or rocky substrates largely unsuitable for seedling establishment (Wein 1981), at least in certain species. Removal of peat also holds consequences for the nutrient status and water retention capacity of remaining soil, which may affect seedling establishment. These habitat changes may be compounded by further soil losses from the erosive effects of subsequent rainfall and frost heave (Wein 1981). Landscapes subjected to such fires may thus remain uninhabitable to certain plants over long time scales. The consequences of habitat change by peat fires has received some attention in the northern hemisphere (e.g. Tallis 1987, Maltby et al. 1990), however, data for Australian peat landscapes are scarce (Wein 1981).

Several coniferous species and *Nothofagus gunnii* have been eliminated from Tasmanian alpine vegetation by catastrophic fires within the last 40 years (Kirkpatrick and Dickinson 1984). These species generally failed to re-establish at the burnt sites, despite availability of seed in adjacent unburnt stands. Similarly, Podger et al. (1988) described the elimination of Tasmanian rainforest dominated by *Phyllocladus aspleniifolius* and *Agastachys odorata* by a single fire in 1881 and its subsequent replacement by sedgeland. Palynological evidence suggests there may be many instances where catastrophic elimination of alpine conifers, *N. gunnii* and species of cool temperate rainforest is not followed by re-establishment, despite fire-free periods of decades or centuries (e.g McPhail 1979, 1981). Failure of these species to re-establish has been attributed partly to soil degradation through erosion and loss of peat and nutrients, partly to poor dispersal of seeds and partly to competitive exclusion by shorter-lived shrub species (Kirkpatrick and Dickinson 1984). However, the relative roles of these factors are not known and require experimental investigation.

There is circumstantial evidence that fires may also mediate extinctions through habitat change (Mechanism 3c, Table 1) in tropical and arid environments. In arid rangelands, mulga (*Acacia aneura*) occupies groves where soils are deeper and more fertile than those occupied by hummock grasses (*Triodia* spp.) (Tongway and Ludwig 1990, Bowman et al. 1995). Bowman et al. (1995) suggested that soil erosion resulting from severe fire followed by intense rain may convert stands of mulga to grassland by creating unsuitable soil conditions for establishment of the former. Stands of tropical monsoon forest have apparently been eliminated by fire regimes involving frequent and/or intense fires (Russell-Smith 1985). Repeated fires cause weakening and eventual death of the dominant tree, *Allosyncarpia ternata*, and its replacement by more flammable grasses and shrubs (Russell-Smith and Dunlop 1987). Conversely, expansion of *A. ternata* into surrounding savanna is thought to be very slow due to intolerance of its seedlings to exposed microclimates and fire (Russell-Smith and Dunlop 1987).

Mechanism 3d

Fire regimes may influence decline of plant populations through high seedling mortality caused by post-fire predation (Mechanism 3d, Table 1). By triggering a transition to seedlings, fires transform the structure of plant populations into a state that is predisposed to much higher levels of mortality than they would otherwise experience because seedlings and vegetative recruits are generally more palatable and more accessible to predators and have less capacity for recovery from herbivory than foliage of established plants (Cremer 1969, Purdie 1977b, Leigh and Holgate 1979, Dickinson and Kirkpatrick 1986, Leigh et al, 1987, Wimbush and Forrester 1988). The extent to which these effects may be offset by predator satiation and post-fire reduction of predator populations is apparently influenced by characteristics of fire behaviour (see text on Mechanism 5c).

Greater losses to predation may be expected after fires, such as those with low scorch heights and little soil heating, that result in relatively low levels of seed release or seedling emergence, since predator populations are less likely to be satiated. The size and patchiness of the burnt area also appears to be an important factor influencing the impact of predation. Predators are more likely to congregate in high densities and may forage more exhaustively within post-fire vegetation when the area burnt is small and/or patchy than when the area burnt is large and/or less patchy. Small, patchy, low intensity fires have been shown to cause greater mortality of seeds (Mechanism 2d, Table 1), seedlings and vegetative regrowth (Mechanism 3d, Table 1) than after larger, less patchy, high intensity fires as a consequence of both invertebrate (Whelan and Main 1979) and vertebrate (Dickinson and Kirkpatrick 1986, Whelan 1986) predators in forests, woodlands and heathlands. However, it is important to emphasise the highly variable nature of predation (Lowman 1985) which limits the portability of research findings between species, sites and different times (Williams et al. 1994, Whelan et al. this volume). Factors that influence variability in predation are inadequately investigated and include palatability and quantity of food availability, the timing and spatial pattern of food availability, the availability and palatability of alternative food sources, weather and social behaviour of the predators (e.g. Ashton 1979, Andersen and Ashton 1985, Lowman 1985, Lowman and Heatwole 1987, Landsberg 1988, Andersen 1989).

Interruption of Maturation and Developmental Growth

There are two mechanisms of population decline and extinction whereby fire regimes interrupt the transfer of individuals from the juvenile life stage to the mature stage (Fig. 1). They involve the effect of frequent fire, respectively, on obligate seeders (Mechanism 4a, Table 1) and resprouters (Mechanism 4b, Table 1).

Mechanism 4a

The rate at which seed banks are replenished after fire depends on the time required for seed production to commence and the subsequent rate of seed production. Gill (1975) distinguished the time required for post-fire seedlings to mature and produce their first flowers, the 'primary juvenile period', from the time required for pre-fire plants that survive complete leaf scorch to recommence flowering, the 'secondary juvenile period'. Both primary and secondary juvenile periods vary between and within species. In resprouters, the primary juvenile period is generally longer than the secondary juvenile period (Bradstock and Myerscough 1988, Keith 1991). In general, primary juvenile periods are longer for woody species than herbaceous species (Benson 1985b, Keith 1991) and longer for woody resprouters than woody obligate seeders (Bradstock 1990, Keith 1991, Auld unpubl. data). Primary juvenile periods of obligate seeders range from less than six months for herbs such as *Gonocarpus micranthus* (Keith 1991) up to twenty years for trees such as *Eucalyptus regnans* (Ashton 1976), while secondary juvenile periods are less variable (Table 3).

TABLE 3

Primary (1) and secondary (2) juvenile periods for selected plant species. (Acacia species in mallee examined by Bradstock (1989) include A. rigens, A. wilhelmiana, A. brachybotrya and A. havilandii).*

Species	Habit	Juvenile Period (yrs)	Source
Obligate Seeders			
Acacia spp. (mallee)*	shrub	2–4 (1)	Bradstock 1989
Acacia myrtifolia	shrub	3 (1)	Keith 1991
Acacia suaveolens	shrub	1 (1)	Auld and Myerscough 1986
Cryptandra ericoides	shrub	3 (1)	Benson 1985b, Keith 1991
Eucalyptus regnans	tree	15–20 (1)	Ashton 1976
Banksia ericifolia	shrub	5 (1)	Bradstock and O'Connell 1988
		7–8 (1)	Benson 1985b
Callitris verrucosa	tree	11–13 (1)	Bradstock 1989
Dillwynia floribunda	shrub	3 (1)	Keith 1991
Dillwynia retorta	shrub	5 (1)	Benson 1985b
Epacris microphylla	shrub	5 (1)	Keith 1991
Epacris obtusifolia	shrub	3 (1)	Keith 1991
Epacris pulchella	shrub	6 (1)	Benson 1985b
Eriostemon buxifolius	shrub	5 (1)	Benson 1985b
Gonocarpus micranthus	herb	0.5 (1)	Keith 1991
Gonocarpus teucrioides	shrub	2–4 (1)	Benson 1985b
Grevillea buxifolia	shrub	8 (1)	Benson 1985b
Hemigenia purpurea	shrub	2 (1)	Benson 1985b
Leptospermum laevigatum	shrub	5 (1)	Burrell 1981
Mitrasacme polymorpha	shrub	2–3 (1)	Benson 1985b
Opercularia varia	herb	2 (1)	Keith 1991
Petrophile pulchella	shrub	4 (1)	Bradstock and O'Connell 1988
		6–9 (1)	Benson 1985b
Poranthera ericifolia	herb	1 (1)	Benson 1985b
Triodia irritans	grass	3–5 (1)	Bradstock 1989
Woollsia pungens	shrub	3 (1)	Benson 1985b
Resprouters			
Aotus ericoides	shrub	>5 (1), 3 (2)	Keith 1991
Banksia oblongifolia	shrub	>17 (1), 2 (2)	Keith 1991
		>23 (1), 1–2 (2)	Zammit and Westoby 1987b
Boronia parviflora	shrub	>5 (1), 1 (2)	Keith 1991
Epacris paludosa	shrub	5 (1), 1 (2)	Keith 1991
Eucalyptus obstans	shrub	>15, 4 (2)	Keith (unpubl.)
Goodenia dimorpha	herb	>6 (1), 1 (2)	Keith 1991
Isopogon anemonifolius	shrub	>7 (2), 2 (2)	Keith 1991
Melaleuca uncinata	shrub	15–20 (1), 5–7 (2)	Bradstock 1989
Mitrasacme polymorpha	herb	5 (1), 1 (2)	Keith 1991
Xanthorrhoea resinifera	shrub	>21 (1), 1 (2)	Keith (unpubl.)

Seed production may reach a peak rapidly after maturation and then decline, or build gradually from low levels to a maximum over several seasons. Contrasting examples include: *Acacia suaveolens*, in which seed production reaches a maximum of 10–21 fruits per plant per year at age 2–3 years and declines asymptotically to less than 4 fruits per plant in 14–16 year-old plants (Auld and Myerscough 1986); and *Banksia cuneata* which reaches maturity at five years of age, establishes a modest seed bank (average of 18 seeds per plant) between ages five and 12 and builds a superabundant seed bank (over 17 000 seeds per plant) by age 25 (Lamont et al. 1991).

Primary juvenile periods and rates of seed production vary between populations within species according to environmental conditions, particularly habitat productivity and post-fire rainfall. In general, longer juvenile periods and slower rates of subsequent fruit production are associated with less productive habitats and low levels of post-fire rainfall than the reverse conditions (Bradstock and O'Connell 1988, Cowling et al. 1990, Keith unpubl. data).

Decline and elimination of plant populations whose fruit production is interrupted by frequent fires (Mechanism 4a, Table 1) has been documented in a wide range of fire-prone habitats (Gilbert 1959, Jackson 1968, Ashton 1976, Siddiqi et al. 1976, Gill 1981, Benson 1985b, Fox and Fox 1986, Nieuwenhuis 1987, Bradstock and O'Connell 1988, Lamont and Barker 1988, Burgman and Lamont 1992, Morrison et al. 1995, Gill and Bradstock 1995, Cary and Morrison 1995). The rate of decline will be most rapid, possibly resulting in local extinction after a single short fire interval, in populations in which all standing plants are killed when scorched and in which the seed bank is completely exhausted by a single fire. The best-known examples of this response are obligate seeders with serotinous seed banks such as *Eucalyptus regnans, Hakea teretifolia, Banksia ericifolia, B. prionotes, B. leptophylla, B. cuneata, Allocasuarina distyla* and *Leptospermum laevigatum* (Ashton 1976, Siddiqi et al. 1976, Burrell 1981, Niewenhuis 1987, Bradstock and O'Connell 1988, Lamont et al. 1991, Pannell and Myerscough 1993, Morrison et al. 1995, Cary and Morrison 1995).

If some proportion of the pre-fire standing plant population survives fire (as in resprouters) or if some proportion of the seed bank remains dormant after fire, then decline that results from interruption of seed production by frequent fire (Mechanism 4a, Table 1) is likely to be less rapid than in populations without these characteristics. Populations of resprouters are rarely eliminated by a single short fire interval, but may decline at a slower rate if deaths of established plants are not replaced by new recruits (Fig. 1, see below). The retention of residual post-fire seed banks may be another buffer against short-term elimination by fires that occur frequently enough to preclude or limit seed production (Noble and Slatyer 1980). In general, serotinous seed banks are completely exhausted by a single fire (e.g. Gill and McMahon 1976, Bradstock and Myerscough 1981, O'Dowd and Gill 1984). In contrast, a residual proportion of soil seed banks may be retained in a dormant state, depending on penetration of heat and smoke derivatives during and after fire, thus providing a capacity for seedling recruitment after a subsequent fire even if no new seeds are produced (Auld 1987a, Auld and O'Connell 1991, Dixon et al. 1995). However, some species with soil seed banks apparently retain few viable seeds after fire (Meney et al. 1994) or at certain times of their annual cycle (Morgan 1995a) and may therefore have limited potential for recovery even if a single short fire interval is followed by longer intervals.

Mechanism 4b

In resprouters and fire tolerators, the time it takes for seedlings to develop fire resistant structures (lignotubers, thick bark, rhizomes, protective leaf bases, corms, buried buds, etc.) is demographically analogous to the primary juvenile period in obligate seeders. If successive fires occur at intervals of less than this duration, then new recruits to the population will be killed without contributing to future generations. Thus population size will decline if recruitment is insufficient to replace deaths of established plants (Mechanism 4b, Table 1).

Vegetative structures that enable resprouting and fire tolerant plants to survive the passage of a fire may remain undeveloped for several years during the juvenile stage of the life cycle, leaving the plants vulnerable to fire during this period (Fig. 1). A positive relationship between post-fire survival and lignotuber size has been demonstrated in species of *Eucalyptus, Banksia, Isopogon, Angophora* and *Telopea* (Noble 1984, Bradstock and Myerscough 1988, Auld 1990, Bradstock 1995). Bradstock and Myerscough (1988) found that juveniles of *B. serrata* and *I. anemonifolius* failed to survive fire if their lignotubers were less than 4 cm and 2 cm diameter, respectively. The fastest growing lignotubers of *B. serrata* reached this critical size at age 5–7 years and a large proportion were predicted to reach it by age 10 years (Table 4, Bradstock and Myerscough 1988). However, in *I. anemonifolius* no 5 year-old juveniles survived fire and only a small proportion of lignotubers were predicted to reach their critical size for survival by age 15 years (Table 4, Bradstock and Myerscough 1988). Observations on other species fall within this range (Table 4), suggesting that the development of fire-resistant lignotubers in a significant proportion of a seedling cohort takes between 6 and 15 years. Observations and inferences of some authors (e.g. Henry and Florence 1966, Zammit and Westoby 1987b) suggest more rapid lignotuber development in some species, however their data do not allow direct comparison with values in Table 4.

TABLE 4

Post-fire survival in juvenile and adult plants of woody species. Age is in years and corresponds to time since previous fire except in T. speciosissima *where 1-and 6-year old cohorts emerged 3 years after previous fire. The age of juveniles of* E. dalrympleana, E. dives *and* E. pauciflora *is not known, but the previous fire was >45 years before the experimental burn. Size is diameter of lignotuber (cm) for all species except* X. resinifera, *number of leaves. Fire severity: low — scorch and partial consumption of ground fuel and shrub foliage; high — complete consumption of ground fuel and shrub foliage. Response based on observed samples except * predicted from size of smallest survivor and mean growth rate (see Bradstock and Myerscough (1988) for method). Sources: Noble (1984) for* E. dalrympleana, E. dives *and* E. pauciflora*; Bradstock and Myerscough (1988) for* B. serrata *and* I. anemonifolius*; Auld (1990) for* A. hispida*; Bradstock (1995) for* T. speciosissima*; and Keith (unpubl. data) for* B. oblongifolia, E. obstans *and* X. resinifera.

Species	Age	Size	Fire severity	Response
Angophora hispida	9	1–3	low	37% survived (n = 27)
Banksia oblongifolia	5	1–3	high	12% survived (n = 188)
Banksia serrata	5–7	<4	low–high	nil survived (n = 13)
	5–7	4–5	low	100% survived (n = 3)
	10	>5	low–high	most survived*
Eucalyptus dalrympleana	?	?	high	63% survived (n = 35)
Eucalyptus dives	?	?	high	59% survived (n = 59)
Eucalyptus obstans	5	0.5–1	high	<1% survived (n = 126)
Eucalyptus pauciflora	?	?	high	59% survived (n = 49)
Isopogon anemonifolius	5–7	<0.5	low–high	nil survived
	10	c. 1	low	nil survived*
	15	c. 2	low	small proportion survived*
Telopea speciosissima	1		high	nil survived (n = 93)
	6		high	22% survived (n = 50)
Xanthorrhoea resinifera	5	1–4	high	38% survived (n = 141)

Few data are available for species with other kinds of recovery organs. In *Xanthorrhoea*, recovery is by continued growth of an apical shoot that is insulated from heat by crowded leaf bases and, in subterranean species, soil. After germination the apical shoot is drawn below the soil surface by contractile roots. Gill (1981) estimated the rate of downward movement to be up to 1 cm per month in cultivated seedlings of *X. australis*. The rate at which apical buds of juvenile plants are drawn down in the field is likely to be slower. However, this mode of recovery may be attained more quickly than development of lignotubers in woody dicotyledonous species. Survival in five year-old cohorts of *X. resinifera* plants was 38% after a fire that consumed all ground fuel and shrub foliage (Table 4). As discussed earlier, some arborescent obligate seeders may survive fires passively by avoiding exposure of tissues to lethal temperatures through development of thick bark and an arborescent habit (see text on Death of Standing Plants and Seeds). The rate at which juveniles develop sufficient bark thickness and canopy height to tolerate fires of various scorch heights is not known, but likely to be more than a decade.

The response of resprouters to frequent fire regimes (Mechanism 4b, Table 1) is analogous to decline of populations of obligate seeders under frequent fire (Mechanism 4a, Table 1), but differs in two important aspects. First, comparison of values in Tables 3 and 4 indicate that seedlings of obligate seeders become reproductive earlier than seedlings of resprouters develop fire-resistant structures. Thus, fire regimes that involve fire intervals long enough to maintain stable populations of most obligate seeders may still cause declines in populations of resprouters, at least woody species. For example, under recurring fire intervals of 10–12 years populations of *Isopogon anemonifolius*, a resprouter, are predicted to decline (Bradstock 1990), while populations of *Petrophile pulchella*, a co-occurring obligate seeder, are likely to remain stable or increase (Bradstock and O'Connell 1988). Second, rates of decline are likely to be slower in resprouters than obligate seeders and are more likely to be reversed by a single long fire interval that provides a window of opportunity for recruitment (Bradstock 1990). This is because the pool of established plants that survive fires in resprouters provide a capacity for population recovery that is not present in obligate seeders, even though this pool may diminish rapidly when high fire frequency is sustained (see text on Death of Standing Plants and Seeds). The nature of these differences between the responses of resprouters and obligate seeders to frequent fire regimes has lead to the perception that resprouters are generally more resilient to frequent fire than obligate seeders (e.g. Zammit and Westoby 1987b, Fox and Fox 1986). Indeed, most of the fire-driven extinctions reported in the literature involve elimination of obligate seeders by frequent fire regimes (Gill and Bradstock 1995). However, this may in part reflect an observational bias, since elimination of obligate seeders involves a mechanism often causing abrupt decline, whereas declines of resprouters are likely to involve time scales beyond the scope of many ecological studies.

Failure of Seed Bank Accumulation

Seed bank accumulation involves the transfer of individuals from the mature stage to the seed stage (Fig. 1). When a seed bank fails to accumulate, seedling recruitment may be limited and a plant population may decline at a rate determined by the death rate among standing plants. Fire regimes may influence such declines directly through the role of fire as a cue for seed production, or indirectly through an interaction with predation during and after production and release of seeds. In the first instance seed production may be limited by infrequent fire regimes (Mechanism 5a, Table 1) or by fires that occur consistently in seasons that do not provide the appropriate cue to stimulate mass flowering (Mechanism 5b, Table 1). In the second instance, a high proportion of seeds produced may be consumed by predators after fires of low intensity, high patchiness or limited spatial extent (Mechanism 5c, Table 1).

Mechanism 5a

The passage of a fire stimulates flowering and subsequent seed production (Fig. 1) in a range of plant species that also have transient seed banks, whereby seeds either germinate soon after their release or lose viability in a short time (Gill 1981, Auld 1994). In some of these species flowering is extremely restricted in the absence of fire so that opportunities for seedling recruitment are essentially constrained to a short period after post-fire seed release (Gill and Ingwerson 1976, Lamont and Downes 1979, Auld 1987b, Lamont and Runciman 1993, Johnson et al. 1994, Lunt 1994, Bradstock 1995). When fires occur infrequently, there will be few opportunities for flowering and seedling recruitment so that populations will decline at a rate determined by mortality among standing plants (Mechanism 5a, Table 1). This type of decline is analogous to that which occurs in response to low frequency fire regimes in species whose seed release or germination is cued to fire (Mechanism 2a).

Many of the Australian species that may be affected by such declines are from monocotyledonous families, although a few dicotyledonous taxa also have essentially obligate pyrogenic flowering (Table 5, Gill 1981). On other continents, pyrogenic flowering is well represented among geophytic members of the Amaryllidaceae, Iridaceae, Liliaceae (*sensu lato*) and Orchidaceae (Kruger 1977) in South Africa and in the Poaceae of North America (e.g. Daubenmire 1968) and New Zealand (e.g. Rowley 1970).

TABLE 5

Resprouting plant species in the Sydney region that flower abundantly only after fire. See Gill (1981) for further examples.

Species	Family	Source
Angophora hispida	Myrtaceae	Auld 1987b
Baumea teretifolia	Cyperaceae	Keith 1991
Baumea rubiginosa	Cyperaceae	Keith 1991
Blandfordia nobilis	Phormiaceae	Keith 1991, Johnson et al. 1994
Chorizandra cymbaria	Cyperaceae	Keith 1991
Chorizandra sphaerocarpa	Cyperaceae	Keith 1991
Cyathochaeta diandra	Cyperaceae	Keith 1991
Deyeuxia decipiens	Poaceae	Keith 1991
Drosera binata	Droseraceae	Keith 1991
Genoplesium filiforme	Orchidaceae	Keith, unpubl. obs.
Haemodorum corymbosum	Haemadoraceae	Keith 1991, unpubl. data
Lepidosperma neesii	Cyperaceae	Keith, unpubl. data
Lomatia silaifolia	Proteaeae	Keith 1991
Prasophyllum australe	Orchidaceae	Keith 1991
Prasophyllum brevilabre	Orchidaceae	Keith 1991
Prasophyllum elatum	Orchidaceae	Keith, unpubl. obs.
Ptilothrix deusta	Cyperaceae	Keith 1991, unpubl. data
Telopea speciosissima	Proteaceae	Pyke 1983, Bradstock 1991
Villarsia exaltata	Menyanthaceae	Keith 1991
Xanthorrhoea media	Xanthorrhoeaceae	Keith, unpubl. data
Xanthorrhoea resinifera	Xanthorrhoeaceae	Keith 1991, unpubl. data

The fire-related cues that stimulate flowering may vary among species, and apparently include ash bed effects, hormonal responses brought on by leaf removal or ethylene, and release from the effects of neighbouring plants and litter. In *Xanthorrhoea australis* 67–87% plants were stimulated to produce inflorescences when subject to burning, leaf clipping or exposure to ethylene (a constituent of smoke and product of injured tissues) relative to 37% in untreated plants (Gill and Ingwerson 1976). In some other *Xanthorrhoea* species fruit production is close to zero at post-fire periods of greater than

2 years (Keith unpubl. data). In *Blandfordia nobilis* post-fire inflorescence production was greatest in the first post-fire year (50–68% plants flowering) and diminished over 3–4 years and correlated with changes in soil chemistry (Johnson et al. 1994). In *Anigozanthos pulcherrimus* and *Macropidia fuliginosa* flowering was enhanced experimentally in the field by burning or by fertiliser application, and to a lesser extent by leaf clipping and clearing of adjacent litter and plant material, relative to untreated controls, but flowering was not enhanced by application of ash or heat (Lamont and Runciman 1993). Inflorescence production was greatest in the first year after fire (10–70% culms flowering) and declined sharply to negligible levels after five years (Lamont and Runciman 1993). Daubenmire (1968) and Rowley (1970) ascribed increased flowering after fire in North American prairie grasses and New Zealand snow grass, respectively, to elevated ambient temperature experienced by stem apices during the summer floral inductive period, decreased shading and increased tillering.

Mechanism 5b

Fire regimes that involve a succession of cool-season fires may fail to stimulate prolific flowering in some species, or at least delay flowering and seed release until the second post-fire year. If these ‘sub-optimal’ flowering events result in seedling recruitment at insufficient levels to replace losses of established plants, then a population will decline (Mechanism 5b). This mechanism of decline and extinction remains largely uninvestigated, particularly in geophytic species that remain as dormant subterranean vegetative propagules unless stimulated to emerge and flower by the passage of a fire (e.g. Jones 1988). For these species, further research is needed to test expected declines, which may be slow and cryptic.

Gill (1981) reported an experiment on *X. australis* showing that inflorescence production in the first post-fire year was greater in response to fires in November and February than in response to fires in May and August. However, many more plants in the latter treatments flowered in their second post-fire year. Thus, the principal difference between treatments was that flowering in most plants was delayed by one year after a cool-season fire compared with a warm-season fire. The delay in seed availability may have implications for seedling establishment (see text on Failure of Seedling Establishment). Experimental observations on *X. media* show that more plants were stimulated to flower in the first two years after a fire in January than in the first two years after a fire in October (Keith, unpubl. data). A prolific flowering response in the South African iris, *Watsonia pyramidata* (>50% ramets flowering), occurred in response to autumn and possibly late summer fires, but not in response to spring fires (Kruger 1977). After spring fires, flowering remained at levels typical of unburnt vegetation (c. 5% of ramets flowering) or less.

Mechanism 5c

Predation may limit the number of viable seeds in the seed bank even in cases where the production of large quantities of seed may have been initiated. When predation consistently limits the availability of seed for germination and recruitment, a population may decline at a rate determined by the death rate of standing plants (Fig. 1). Fire regimes may affect the impact of predation on seed availability by influencing the relative abundance of predators and their food source (Mechanism 5c, Table 1).

The passage of certain fires that maximise the quantity of seed released relative to predator abundance may be critical in the avoidance of this mechanism of decline in many plant species whose spontaneous rate of production or release of seeds is small compared with the maximum post-fire rate or where the post-fire rate of seed production and release varies depending on aspects of fire behaviour. Species potentially affected have palatable seeds and include those with serotinous seed banks, those with a pyrogenic flowering response and some short-lived obligate seeders whose germination and emergence is constrained by the timing of fire (e.g. Pate et al. 1985). In such cases predator populations may be satiated by a superabundance of seeds caused by massive post-fire seed release, allowing greater numbers to escape predation and germinate than in unburnt conditions (Ashton 1979, O'Dowd and Gill 1984, Auld and Myerscough 1986, Andersen 1988). A similar outcome (i.e. temporary increase in edible seeds per predator) may be achieved if fire reduces the density of predator populations. This appears to be the case in species of Lepidoptera (Friend 1995), some of which, in their larval stage, are pre-dispersal predators of developing seeds and fruits (Gill 1981 and unpubl., Zammit and Hood 1986, Lamont and van Leeuwin 1988, Wallace and O'Dowd 1989).

When seeds are released spontaneously, the availability of seeds more closely matches the ability of predators to consume them because seed release occurs at a slower rate than immediately after the passage of a fire (O'Dowd and Gill 1984, Auld 1987b, Bradstock and O'Connell 1988, Bradstock 1990, Witkowski et al. 1991, Lamont et al. 1991). Rates of seed removal by predatory animals in unburnt vegetation vary up to 100% within a few days of experimental placement and have been shown in a variety of species and habitats to be significantly greater than rates of removal immediately after certain fires (Ashton 1979, O'Dowd and Gill 1984, Abbott and van Heurck 1985, Andersen and Ashton 1985, Wellington and Noble 1985b, Andersen 1988, Auld 1995a, Pannell 1995). The effect of predation is thus to strengthen the dependence of recruitment on fire-related cues for flowering (Mechanism 5a and 5b, Table 1), as well as seed release and germination (Mechanisms 2a–2d, Table 1).

Fires may vary in the extent to which predator satiation is effected, depending on fire characteristics. Greater losses to predation may be expected after fires with low flame heights, little soil heating and patchy spatial pattern because such fires result in relatively low levels of seed release and germination so that predator populations are less likely to be satiated. While empirical evidence for this effect refers primarily to seedlings and vegetative recruits (Whelan and Main 1979, Whelan 1986, Dickinson and Kirkpatrick 1986), analogous effects involving seeds have been inferred (Gill 1981, Bradstock and Bedward 1992, Auld et al. 1993) and warrant further investigation.

Other Mechanisms of Decline and Extinction

There may be other mechanisms of plant population decline and extinction related to fire regimes that are, at present, poorly known. Some of these may involve complex biological interactions between plants, other organisms and fire, such as mutualistic relationships (e.g. Lamont 1995) and pathogenic relationships (e.g. Shea 1979, Keith 1995a).

Lamont (1995) described mutualistic relationships in eucalypt forests between fungi, terrestrial marsupials and woody understorey plants that were mediated by fire. Seedling growth of various shrub species is curtailed in the absence of the fungi which form mycorrhizae enhancing uptake of nutrients. Dense groves of these shrubs provide essential shelter for marsupials, which also depend on the sporocarps of the fungi for a food source, particularly after fire. The fungi, whose sporocarps are subterranean, depend on the marsupials for spore dispersal and possibly for digestive pretreatment for spore germination. The fungi also depend on their plant hosts for organic nutrition. Fires interact with all components of this partnership: the canopies of shrubs are consumed; fungal mycelia in the litter layer are consumed; soil seeds are stimulated to germinate and fungi may be stimulated to sporulate; a proportion of the marsupial population may be killed; but their enhanced foraging activity in the days after fire disperses fungal spores and enhances inoculation of post-fire seedlings which grow rapidly to restore shrub cover (Lamont 1995). Clearly, fire regimes that cause declines in any one component of the partnership (e.g. through poor germination of soil seed, high levels of marsupial mortality, etc.) may also cause declines in populations of the other organisms.

Pathogenic interactions are another mechanism of decline or extinction of plant populations that is potentially influenced by fire. The introduced pathogenic root-rot fungus, *Phytophthora cinnamomi*, causes high levels of mortality among some tree and shrub species in temperate Australia (Weste and Marks 1987). It has been suggested that the impact of the pathogen may be controlled by reducing the abundance of its major hosts (Shea 1979). Abbott (1985) and Burrows (1985) have explored how populations of one such host, *Banksia grandis*, may be reduced through management of fire regimes. Conversely, Burdon (1991) argued that there is little possibility of any susceptible plant species escaping disease through low density because of the pathogen's extreme aggressiveness, wide host range and persistence in the soil after invasion. It has also been suggested that the timing of fire after invasion is critical to the recovery of species with soil seed banks (Keith 1995a). Soil seed banks may provide a 'refuge' in which some individuals of a population evade death during the initial phase of the disease epidemic. With time after invasion, the abundance of the pathogen and hence its effects on standing plants apparently decline (Weste and Ashton 1994). The passage of a fire after decline of the pathogen population, but before soil seed is lost through senescence, may allow replenishment of the standing plant population by stimulating germination from the soil seed bank (Keith 1995a). The interactions between fire regimes, plant populations and their fungal pathogens clearly warrant more research.

VEGETATION DYNAMICS AT HIGHER LEVELS OF ORGANISATION

Whole Plant Populations, their Habitats and Associated Species

Much of the preceding discussion has focussed on processes that operate within various parts of the plant life cycle (Fig. 1, Table 1). These processes do not act independently of one another and, at higher levels of organisation, this has consequences in physical and biotic environments that are heterogeneous in space and time. Explicit mathematical models and computer simulations (see below) are powerful tools for predicting the outcomes of these interactions which may be compensatory, favouring population stability, or complementary, favouring accelerated rates of increase or decline. High intensity fires in mature wet temperate eucalypt forests provide one example where opposing effects may produce a neutral outcome in terms of population persistence and community composition (Ashton 1981). On one hand these fires cause high levels of mortality among standing plants, and on the other hand, they stimulate high levels of seedling establishment through mass seed release, predator satiation, and diminished effects of resource limitation, competitors and pathogens. Indeed without such fires populations of these eucalypts may eventually decline to extinction through senescence (Gilbert 1959, Ashton 1981).

When life-cycle processes interact in a complementary manner, the risk of extinction may be amplified. Consider, for example, populations of woody plants subject to a fire regime comprising frequent, low intensity, patchy fires which occur invariably just before a dry season. Multiple mechanisms of decline and extinction may operate under such a regime. Depending on the life-history characteristics of the species these may include: decline of standing plant numbers through depletion of stored buds and starch or structural weakening (Mechanism 1d) or through weed competition (Mechanism 1g); low rates of germination and seedling emergence due to slow rates or low levels of seed release (Mechanism 2b) or to low rates of release from dormancy (Mechanisms 2c and 2d); low rates of seedling survival due to desiccation (Mechanism 3b) or predation (Mechanism 3d); interruption of maturation (Mechanism 4a) or the development of fire resistant structures (Mechanism 4b) in juvenile plants; and depletion of the potential seed bank by predation (Mechanism 5c). Decline and extinction may be expected to eventuate more rapidly when these mechanisms are considered as operating concurrently on different parts of the plant life cycle (Fig. 1) than if they are considered to operate in isolation.

Many of the examples of plant extinctions cited by Gill and Bradstock (1995) were related to variations of the above scenario. Indeed, fire regimes that involve frequent fire, fires resulting in little vertical penetration of heat (and possibly smoke derivatives) and fire exclusion are associated with multiple mechanisms of decline and extinction (Table 1) and therefore must be the foci of fire management for conservation. At higher levels of organisation, these types of fire regimes have been widely implicated in the simplification of vegetation structure and the loss of ecosystem diversity, particularly through local extinctions of woody plants (e.g. Gilbert 1959, Siddiqi et al. 1976, Fox and Fox 1986, Clark 1988, Morrison et al. 1995, Clark and Morrison 1995) and their dependent biota (e.g. Rowley and Brooker 1987, Lindenmayer et al. 1990, Catling 1991, York 1993).

Metapopulation dynamics: environmental correlations and dispersal among populations

The significance of any given extinction must be measured in terms of its spatial and genetic scales. Local extinctions may be of little consequence to conservation of metapopulations and species if they result in no net loss of genetic diversity and are balanced over some relevant time scale by establishment of new populations. Dynamics of this type may be expected in organisms with a panmictic metapopulation structure and widely dispersed propagules. Possible examples are mistletoes and short-lived wind-dispersed Asteraceous species known as fire weeds. Conversely, local extinctions may be of great significance in species with poor dispersal capability or with a high proportion of genetic diversity apportioned between, relative to within, their populations.

The spatial arrangement of populations in a landscape will influence whether different populations share similar fire regimes. Populations in close geographic proximity and aligned to common fire pathways are more likely to share a common fire regime than if they are separated by large distances or by significant barriers to fire spread (e.g. expanses of water or developed areas). Populations in close proximity are also more likely to share similar post-fire environmental conditions and similar predator pressures that may influence the likelihood of their decline and extinction (Mechanisms 3b, 3d and 5c) than populations separated by larger distances. When different populations are likely to experience the same fire events, droughts, predator fluxes, etc., their probabilities of extinction will be correlated, resulting in a higher probability of extinction for the entire metapopulation than if all populations had independent probability of extinction (Burgman et al. 1993).

The importance of dispersal in the persistence of metapopulations cannot be overemphasised (Burgman et al. 1993), yet data on dispersal of plants are conspicuously scarce in the literature. For species in which all effective seed dispersal occurs immediately after fire, Bradstock et al. (in press) have shown that the spatial extent of fire mediates the persistence of populations within landscapes by influencing the amount of seed released and the extent of habitat available for establishment. The probability of seed dispersal to neighbouring patches in their model was critical to population persistence.

Average dispersal distances may be limited to a few metres or tens of metres in a large majority of species in the Australian fire-prone flora, particularly species that have heavy winged propagules or smaller propagules without wings or hairs (e.g. Lamont 1985, Wellington and Noble 1985b, Auld 1986, 1987b, Morgan 1995b, Keith, unpubl. data). Experimental studies on perennial herbs in North America suggest similarly short dispersal distances (e.g. Primack and Miao 1992, Weiblen and Thomson 1995). Longer dispersal distances are possible in species whose propagules are dispersed by wide-ranging vertebrates. Fleshy-fruited species are known to be consumed by frugivorous birds and bats and may be deposited kilometres from their origin after digestion (Date et al. 1991, Eby 1991, Overton 1994). However, fleshy-fruited species are relatively uncommon in the Australian fire-prone flora (French 1991).

Although most studies point to the limited dispersal capability of the fire-prone Australian flora, dispersal of plant propagules over long distances remains conjectural.

Very infrequent long-distance dispersal events are by and large intractable topics for research and may therefore have escaped detection (Levin 1981). Whelan (1986) suggested that the convection column of a fire could promote long-distance dispersal of wind-dispersed seeds, provided propagules were drawn into the updraught without heat damage. Although there appear to be no reports of such occurrences, there are some anecdotal reports of charred and uncharred leaves falling to ground many kilometres from large fires (Whelan 1986, pers. obs.). These events are potentially most important in metapopulation dynamics and gene flow (Portnoy and Willson 1993), but the likelihood that they will lead to establishment of new populations will be further limited by the chance of dispersal to suitable habitats, as well as the factors that limit germination and establishment (see text on Failure of Seed Release and/or Germination and Failure of Seedling Establishment).

FIRE MANAGEMENT FOR CONSERVATION

The wide range of fire regimes associated with mechanisms of decline and extinction (Table 1) pose a quandary for fire managers who may be looking for simple prescriptions to meet conservation objectives. There are many apparent contradictions in the requirements of fire frequency, intensity and season for survival of species coexisting within one community. If, for example, frequent fires may cause declines in some species through interruption of life-cycle processes, while infrequent fires may cause declines in others through senescence or competitive elimination (Table 1), how can extinctions be avoided? Similarly, the season in which fire stimulates greatest vegetative recruitment and flowering and results in least mortality in resprouters (i.e. spring) is apparently the same season in which fire exposes subsequently emerged seedlings to greatest risks of mortality from desiccation (Table 1). A means of addressing such conflicts in fire management is offered firstly by reference to theories of species coexistence and diversity for the development of management principles, and secondly by a wide range of practical tools for experimental management.

Theories of coexistence and diversity

The intermediate disturbance hypothesis states that maximum diversity will be maintained when disturbances of intermediate intensity and size occur at intermediate frequencies (Connell 1978). Many of the fire regimes associated with population decline and extinction reviewed here are indeed associated with extremes in fire frequency, intensity and size (Table 1). It follows that avoidance of these extremes in fire management should minimise the chance of extinctions and favour maintenance of diversity (Hobbs and Huenneke 1992). Floristic diversity may be maintained by promoting fire intervals that are intermediate between the time of maturation and the time of senescence (Hobbs and Huenneke 1992). However, the fire requirements of some co-existing species may not overlap when defined in this manner (e.g. Keith and Bradstock 1994, Keith 1995b), so that sustained, invariant intermediate regimes of fire, in themselves, may be insufficient to maintain full diversity (van Wilgen et al. 1994).

In the mosaic paradigm the focus of fire management is maintenance of diversity within heterogeneous landscapes. In other words, the goal of conservation is maintenance of species somewhere within a landscape, but not necessarily at all inhabitable sites or at any one site continuously. Thus different fire regimes may be prescribed for different parts of the landscape to ensure conservation of different components of the biota. Species may either persist within a subset of patches or persist in some dynamic equilibrium by migrating from patch to patch as the suitability for habitation of patches changes through time.

Maintenance of fire mosaics, in particular those involving patches of different post-fire ages, has been widely advocated and applied in Australia, particularly for fauna conservation (e.g. Saxon 1975, Christensen and Kimber 1975, Bradstock et al. 1995). However, implementation of fire mosaics in management has largely been governed by logistical considerations and demands of management goals other than conservation, such as protection of property and timber production (Williams et al. 1994, Bradstock et al. 1995). Consequently, some aspects of deterministically managed fire mosaics such as the size and spatial pattern of patches may not be sufficient to avoid extinctions. As discussed previously, fire patch size may mediate persistence of some plant populations through the outcomes of predation (Whelan and Main 1979) and dispersal (Bradstock et al. in press). Hence, some deterministically managed mosaics may involve patches that are too small to maintain populations of some species (McCarthy and Burgman 1995). Williams et al. (1994) and McCarthy and Burgman (1995) point out other features of highly deterministic mosaics as maintained, for example, in production forests that may make them unsuitable for conservation of some species. Further, the assumption that mosaics of patches of different post-fire age help to maintain populations of animal species through dynamic equilibria has been called into question by recent empirical studies (e.g. Short and Turner 1994). Another potential limitation to some systems of mosaic management concerns the role of unplanned fires (Williams et al. 1994, Bradstock et al. 1995). Deterministic mosaic management systems that aim to maintain rigid patch boundaries or fine-scale patterns of fire history are unlikely to be viable in the face of unplanned ignitions and weather conditions of high fire danger (Bradstock and Scott 1995).

Where mosaics concern variability of fire regimes in space, lottery models concern the variability of fire regimes in time. The relevance of lottery theory to fire-prone vegetation has recently been demonstrated by Laurie and Cowling (1995) and Lamont and Witkowski (1995). Its relevance to conservation is predicated upon: differing requirements for survival and establishment among species; and rates of population decline and elimination that are slow relative to the recurrence of recruitment events (Chesson and Warner 1981). Thus a sequence of different recruitment and mortality events that alternately favour establishment in populations of different species may be sufficient to maintain full species diversity (Cowling et al. 1990, Keith 1995b). In practical terms this means that a site must experience fires of varying intensity, season, size and at varying intervals if its full complement of species is to be maintained. Van Wilgen et al. (1994), Bradstock and Scott (1995), Keith (1995) and Bradstock et al. (1995), for example, have stressed the importance of variability in the length of fire intervals, within certain thresholds, for the maintenance of full diversity. Species that decline under say frequent fires could coexist with species that decline under infrequent fires, so long as a favourable fire interval occurred often enough to reverse any trends of population decline before extinction took place. Rates of decline are therefore crucial. A lottery approach to fire management is unlikely to be successful where single fires may cause sudden elimination (e.g. Mechanism 3c, Kirkpatrick and Dickinson 1984). Further, it should be recognised that some of the environmental viability required for lottery coexistence, such as landscape pattern, post-fire weather conditions and aspects of fire behaviour under certain conditions, may be influenced only partly through management.

Practical Tools for Decision Support in Experimental Fire Management

While each of the three theories has limitations, together they provide some principles for the management of fire for conservation. There are also a number of practical tools that assist in the planning and implementation of fire management in specific areas. General principles could be translated into specific guidelines through the use of thresholds in fire regimes as suggested by Bradstock et al. (1995). Fire regimes likely to cause catastrophic, widespread and long-lasting declines or elimination could be identified in such thresholds which are expressed in terms of the components of the fire regime (i.e. upper and/or lower limits to frequency, intensity, season, type) and its and spatial pattern. Avoidance of fire regimes beyond the thresholds is in accordance with the intermediate disturbance hypothesis. The risk of more subtle declines and extinctions would be reduced by promoting variability in fire regimes within the thresholds. Variability should be on both spatial and temporal scales in accordance with the mosaic paradigm and lottery theory, respectively. Bradstock et al. (1995) give an example of a set of fire regime thresholds for management of a coastal heathland, though these do not address the spatial component of fires.

The extremely high species richness of some fire-prone plant communities may pose a problem for the development of management thresholds (e.g. George et al. 1979, Keith and Sanders 1990, Keith and Myerscough 1993). In such cases data may be available for only a fraction of the species that need to be considered. Functional classifications of species provide one means for effective use of this limited information (Verner 1984). As discussed earlier, such classifications could be constructed using life-history attributes to group species with similar mechanisms of decline and extinction. Examples of the application of such classifications to fire-driven vegetation dynamics are both practical (e.g. Purdie 1977a,b, Keith and Bradstock 1994) and theoretical (Noble and Slatyer 1980, Moore and Noble 1990). Information on life-history attributes, such as ability to resprout and type of seed bank, is available for a wide range of species (Gill and Bradstock 1992) and is easy to obtain in the field (e.g. Keith 1991). Within functional groups, the species most susceptible to decline under particular fire regimes would be the focus for defining thresholds. For example, within a group of serotinous obligate seeders, the primary juvenile period of the slowest maturing species should be considered when defining the upper threshold for fire frequency (Bradstock and Auld 1988, Bradstock and O'Connell 1988).

Predictive models of the dynamics of plant populations and communities are another set of practical tools available to fire managers for the translation of principles into strategies and prescriptions. Models provide powerful tools for understanding the outcomes of complex interactions between life-cycle processes (e.g. Auld 1987a, Bradstock and O'Connell 1988), between species (e.g. Noble and Slatyer 1980, Moore and Noble 1990), in temporally heterogeneous environments (e.g Burgman and Lamont 1992) and in spatially heterogeneous landscapes (e.g. Green 1989, Bradstock et al. in press). Models allow their users to explore the consequences of alternative actions before they are implemented. Through sensitivity analyses, they also allow salient factors for research and management to be singled out from a morass of potentially important variables (Burgman et al. 1993). Models that incorporate stochastic variability in environmental conditions and disturbance regimes are potentially the most useful for decision support in management. These allow risks of extinction associated alternative management options to be assessed explicitly in the face of uncertainty (Burgman et al. 1993, McCarthy and Burgman 1995). Management options may be ranked accordingly. However, predictive ecological models in general are yet to realise their potential in practical fire management, partly because of limited data on life-cycle processes and partly because researchers have had limited success in fostering their wide use among managers.

Knowledge of the local landscape, its biota and its fire history is one of the most important requisites for fire management. Systems of experimental management and monitoring, as proposed for example by Gill and Nicholls (1989), offer a sound framework for the acquisition of such knowledge, as well as a means for ongoing assessment of both fire regimes and biotic responses in relation to the goals of fire management (Bradstock et al. 1995). Hypothesis testing of this kind is an essential but often neglected aspect of natural area management (Murphy 1991). Ongoing assessment and judicious acquisition of knowledge is essential if management is to be flexible and responsive to changes in biota and fire regimes over dynamic landscapes (Bradstock et al. 1995, Keith 1995).

Geographic information systems provide powerful tools for organising this information into a wide range of forms for display, analysis and interpretation (van Wilgen et al. 1994, Garvey this volume). This technology has to a large degree outstripped the availability of spatial information on fire history and vegetation which, in most areas, is unavailable at resolutions and accuracies required for sound ecological decisions in fire management.

CONCLUSION

Many potential mechanisms of plant extinction and the fire regimes with which they are associated have been identified (Table 1). Fire regimes associated with multiple mechanisms of decline and extinction, particularly of woody species (obligate seeders and resprouters), include high fire frequency, low fire frequency and repeated fires that result poor vertical penetration of heat. However, many other, possibly overlapping, fire regimes may be associated with high risks of extinctions within any given area. Minimisation of these risks by avoiding detrimental fire regimes may therefore be prove to be a complex management task.

Our knowledge of the plant ecology of fire is still deficient on some important aspects. However, existing knowledge on mechanisms of decline and extinction, combined with ecological theories and practical management tools, is enough to predict how some populations and communities of plants may respond in landscapes subject to a wide range of fire regimes. Ongoing acquisition and evaluation of predictive knowledge of this kind are essential for a strong scientific basis for the management of fire for conservation.

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